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OUTLOOK ON AGRICULTURE



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The design in linocut on the cover is a composite of drawings from two medieval manuscripts. In the centre is a figure from the works of Matthew Paris, who entered St. Alban's as a monk in 1217. Surrounding this, depicting farming activities throughout the year, are drawings based on MS. from the Benedictine Abbey of Sweifalten, circa 1162.



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OUTLOOK ON AGRICULTURE

VOLUME III • AUTUMN 1961 • NUMBER 3

PAGE

- 102 *Editorial: Ecology*
- 103 *Nutritional Relationships between Crops and the Soil*
R. SCOTT RUSSELL, M.Sc., M.A., Ph.D.,
D. A. BARBER, B.Sc., Ph.D., and
P. NEWBOULD, B.Sc., B.Agr., D.Phil.
- 111 *Foliar Application of Major Nutrients to Fruit and Plantation Crops*
D. J. HALLIDAY, M.B.E., M.A.
- 115 *The Fruit Fly Problem in Australia*
B. A. B. EDWARDS, B.Sc. (Hons.)
- 122 *Aphids and Aphicides*
D. PRICE JONES, M.Sc., Ph.D., and
E. C. EDGAR, Dip.Hort.
- 131 *Control of Worms in Ruminants by Chemotherapy*
W. T. HARROW, M.R.C.V.S.
- 139 *Control of Worms in Ruminants by Pasture Management*
E. L. TAYLOR, C.B.E., D.V.Sc., M.R.C.V.S., D.V.H., N.D.A., N.D.D.
- 145 *Book Reviews*

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The problems of the agriculturist are never simple, though they may be simplified. Some of those of the experimental scientist in the past were partly solved by changing one factor at a time, an approach that has been superseded, however, by the use of multivariate techniques in many different forms: by the recognition that the interactions of factors are of importance. The farmer has always been conscious that a number of factors intervene in his affairs, and interfere with each other: his attitude to soil and crop and stock has long been and continues to be that of the ecologist.

It is perhaps not surprising, therefore, that rapid progress in agriculture required the development of experimental techniques suited to the many-sided variability of the subject, or that the techniques, once established, found value in other sciences, for complexity is universal rather than exceptional.

Most of the articles in the present number are concerned with problems in which the habits and mode of life of living organisms must be taken into account in relation to the total environment: the ecological situation is strongly emphasised. Some topics are: The selection of pesticides to fight aphids having regard to the complexity of their relationship to crop and surroundings; The control of worms in ruminants by pasture management, and with drugs; The menace of native and introduced fruit flies in Australia. The consideration of relationship is present also in the article dealing with crops, plant nutrients and soil, an article that attempts to show how some of the newer conceptions of the physical chemist and plant physiologist have brought a measure of understanding to many of the intractable agricultural problems of the nineteenth century.

In another field, that of political economics, even the difficulties of the Common Market, with which the agriculturist appears to be so much concerned, might be regarded, not unreasonably, as ecological—problems of relationship and co-existence. The comment of one of our contributors, out of context, is apt: "If we must live with others, we must first get to understand them," and reciprocally be understood by them.

If E.E.C. countries were concerned merely about the production of food their difficulties would not be serious. That food production per acre can be largely increased is widely known, and steady progress is being made throughout the western countries. The themes of our last four editorials are relevant: The world food problem, Fertilizers and food production, More meat and

milk from grass and World food and population. In countries where 80% of income or more must be spent on food, the problems of subsistence are paramount: these are the countries in which the newly launched Freedom from Hunger Campaign will render great service by demonstrating better use of resources. But in the West today only 30% of income is spent on food, and the percentage is falling. As standards of living continue to rise the relative outlay on food will drop still further. Also in the West, with some exceptions that will be remedied, food consumption has reached or even exceeded the level of sufficiency; indeed, not only consumption but also production of many foodstuffs is approaching adequacy.

So the problems of the West are not merely those of producing food but of producing it economically; of avoiding losses and waste; of effective packaging and transport; of marketing; of presentation and salesmanship; and of the more recondite aspects of sound nutrition.

The last theme may be expanded. There is a chain that links nitrogen from the fertilizer factory, through the merchant and farmer, to nitrogen in the essential amino acids present in the protein of milk, meat, vegetables and grain. The chain is a long one, but in the West today it is a lifeline. Ten per cent of the protein constituting the Londoner, it has been estimated, comes from the nitrogen fixation industry—and the figure will increase. The ecological environment of the citizen now includes the fertilizer factory!

The Editorship

On 30th June Mr. E. J. McNaughton relinquished his editorship of OUTLOOK ON AGRICULTURE. His wide knowledge, talent and enthusiasm coupled with hard and conscientious work have been prime factors in the evolution and establishment of the journal.

McNaughton joined Brunner, Mond & Co. (Japan) Ltd. in 1928 and was successively a technical agricultural officer in the Far East and Technical Director of I.C.I. (Malaya) Ltd. He returned to Great Britain in 1934 and worked first at Jealott's Hill Research Station and then in I.C.I.'s Central Publicity Department, London. In 1943 he was seconded to the Ministry of Economic Warfare, becoming consultant in the United States on Far Eastern matters. From 1945 until 1955 McNaughton again worked at Jealott's Hill and built up the Intelligence Section of the Hawthorndale Laboratories. He assumed the editorship of OUTLOOK ON AGRICULTURE in 1955 and on retirement from I.C.I. in 1958 agreed to continue that work.

McNaughton's wide range of interests includes painting, book-binding, gardening and authorship. His many friends will wish him many happy years in which to enjoy to the full the fruits of a lively mind.

Dr. C. C. Tanner has assumed the editorship of the journal. Tanner joined Synthetic Ammonia and Nitrates Ltd., Billingham, as a chemist in 1929. Three years later he transferred to what was to become the General Chemicals Division and worked first at Oldbury and then at Widnes until 1943, becoming Acting Assistant Research Manager; from 1943 to 1945 he was concerned with prospective Divisional post-war development work. He was then appointed head of the Hawthorndale Laboratories at Jealott's Hill and in 1954 joined what has now become the Agricultural Overseas Section of the Billingham Division in London.

NUTRITIONAL RELATIONSHIPS BETWEEN CROPS AND THE SOIL

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(Agricultural Research Council Radiobiological Laboratory, Wantage, Berkshire)

A greater insight regarding the physico-chemical relationships of nutrient elements in the soil, and a better understanding of plant physiology, help to explain many problems that could not be resolved by pioneer agricultural research workers. The way in which nutrients enter plant roots, and the rate-governing processes, are becoming clear, but the seasonal fertilizer responses of crops still remain difficult to forecast with accuracy.

One of the outstanding landmarks in the development of agricultural research was the realization that apart from carbon dioxide, which was absorbed from the atmosphere, the soil was the source of all the raw materials for plant growth. Once this was established the study of plant nutrition could develop on a firm basis. Over a hundred years ago Boussingault initiated the first important field experiments on plant nutrition and shortly afterwards Lawes and Gilbert laid the foundation for the widespread use of fertilizers in agriculture. By modern standards the early experiments lacked precision and more than half a century was to pass before the statistical principles of experimental design were defined. None the less, the methods of the pioneers differed little in principle from those of their more modern successors in agricultural chemistry. Mineral or organic matter was added to the soil and its effect was examined on the yield and composition of the crop and on the quantity of nutrients which could subsequently be extracted from the soil.

Although this approach had great practical value, it was essentially empirical and the underlying principles remained largely obscure. Experience showed that the extraction of soils by certain procedures, for example with solutions of dilute acids or salts, frequently provided a valid basis for estimating the quantities that crops would absorb or for recommending the application of fertilizers. These were, however, qualitative rather than quantitative measures of availability and the factors which determined the accessibility of nutrients to plant roots were most imperfectly understood. An early discovery, still valid, was that the solubility of nutrients is an important factor affecting their entry into plants.

Notwithstanding their achievements the early agricultural chemists were well aware of their limitations. By 1855 it was apparent that, if adequate yields were to be obtained, the quantities of

nutrients added to the soil might greatly exceed the amounts which the plants actually absorbed, especially for phosphate. A large fraction appeared to become "unavailable," particularly in certain soils. But phosphate was not permanently immobilized in forms inaccessible to plants: as research continued it was realized that some benefit remained even after long periods of time.

Fertilizers were already being used on a considerable scale before the physiological processes of plants, which control the absorption of nutrients and their effects on growth, were understood. The credit for establishing the basic principles of fertilizer usage thus lay with the agricultural chemist rather than the plant physiologist, but the co-operation of the latter has become increasingly important. The manner in which plants grow determines not only the quantity of different nutrients absorbed but the ratios in which they are used and the time in the life cycle of the plant when they are most beneficial. Our increasing understanding of the physiology of plants combined with fuller knowledge of the physico-chemical behaviour of nutrients in the soil now makes it possible to explain many of the observations of the pioneers; it also promises the solution of hitherto intractable problems.

THE SOIL AS A SOURCE OF NUTRIENTS FOR PLANTS

The pioneers had recognized that only a fraction of the nutrients in soil was in a form accessible to plants, and that insoluble material could not be directly absorbed. It seemed that nutrients could exist either in "available" or "unavailable" states; great attention was therefore paid to measurement of the "available" fraction in soils. Two types of procedure were widely employed. Plants were grown in small volumes of soil which might be exhausted completely, or nearly so, of mineral nutrients. Alternatively, solvents were devised in

the hope that they would extract only the "available" nutrient fraction. Many such formulations were tried and many are still of practical value. Dilute citric acid for example is widely used to estimate "available" phosphate, while readily exchangeable cations are commonly estimated by displacement with solutions of such salts as ammonium acetate. These procedures are simple to carry out and have proved of great value for the comparison of soils that are similar in nature. Fertilizer practice has been guided largely by the evidence they provide. But no single method can be applied to all soils, and, although the soil chemist from experience may be able to allow for some lack of precision, new procedures are clearly necessary if the factors that determine nutrient availability are to be characterized with accuracy.

The application of thermodynamic principles has greatly increased our understanding of ionic relations in the soil/plant system. It has long been known that sites on solid surfaces of soil particles have considerable affinity for free ions. Exchange equilibria are rapidly attained between these surfaces and the solution phase, ions that migrate between the two phases forming what is commonly described as the "labile" ionic pool. When the balance is upset owing to the entry of ions into plants new equilibria are established by the passage of ions from surfaces into solution. This is demonstrated by the fact that the total quantity of ions absorbed by plants over a prolonged period may greatly exceed that initially present in free solution. It was once thought that the situation might be explained by "contact exchange" in which ions entered plants directly from mineral surfaces [8], but this interpretation has of late been little favoured [9]. It has been found more satisfactory

to accept the model which is illustrated in a simplified form in Figure 1. The necessary requirement for the absorption of ions is that the plant root shall reduce their free energy below that in the ambient medium. Schofield [17] made possible a much improved analysis of these relationships when he proposed that the labile ions in the soil could be characterized by two parameters: their potential and their capacity, these terms being used in the thermodynamic sense. The product of the potential and capacity is the quantity of ions in the pool. The same approach had earlier proved valuable in elucidating the behaviour of water in soils [16]. Plants cannot absorb all the water in the soil; they are unable to absorb when the water tension falls below a certain level, usually called the wilting point. Until, however, the water content of the soil has sunk to the wilting point there is no physico-chemical means of distinguishing water molecules that will eventually enter plants from those that will remain in the soil. Both are part of the same labile pool; it is impossible to distinguish available and unavailable water by any physico-chemical characteristic.

When it was realized that the same concept could explain the behaviour of nutrients in soil, it was easy to understand the failure of extraction methods to provide a valid assessment of the relative quantities of nutrients that a plant will absorb from soils of contrasting type. Extraction procedures displace, with varying efficiency, the content of the labile pool; but it is the potential of the pool, which cannot be measured in this way, that determines the extent of absorption. Thus, if structural differences between two soils cause the relationship between the potential and the capacity of their labile pools to contrast markedly, extraction procedures will not provide valid information on the relative quantities of nutrients that plants can absorb.

The validity of this approach has been supported by investigations of the absorption of phosphates [14]. The use of radioactive phosphorus has made it possible to determine the quantity of ions in the labile pool without undue difficulty by measuring isotopic exchange between soils and solutions. An alternative procedure, employed initially by Larsen [10], is to grow plants in soil containing a known quantity of radioactive phosphorus and to estimate the size of the labile pool from the quantity of inactive soil phosphate with which the tracer is diluted when it enters the plants. The two methods usually give comparable values. If a series of soils,

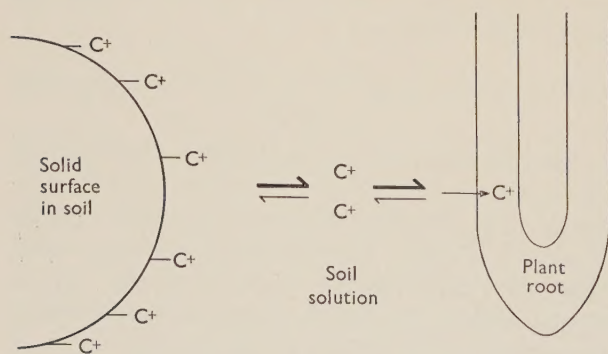


FIG. 1. Ions on solid surfaces are in equilibrium with those in the soil solution from which plant roots absorb. Heavy arrows indicate the direction of net flux when ions are entering plant roots. Comparable relations occur for many anions.

differing only in their phosphate content, is prepared by adding varying quantities of soluble phosphate to the same parent soil, it is found that the amount of phosphate that enters the plants varies closely with the quantity in the labile pool measured by either procedure (Figure 2). The

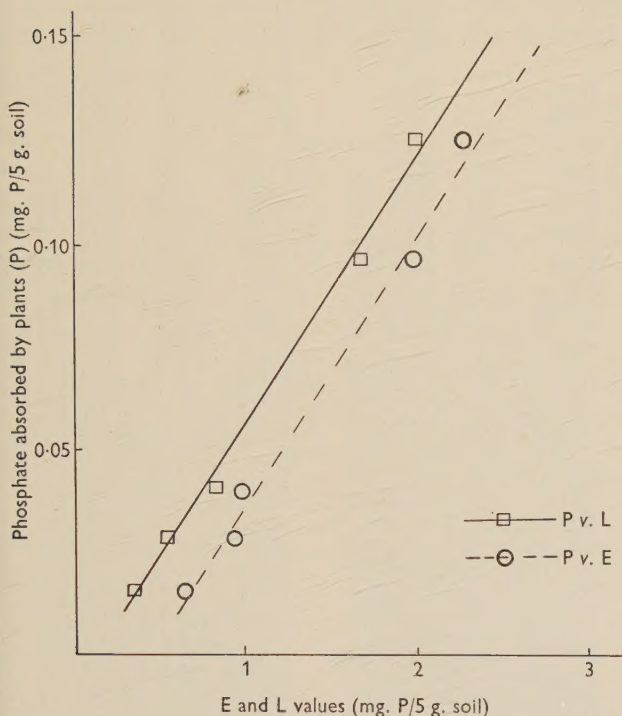


FIG. 2. Relationship between absorption of phosphate by barley plants in 43 days (P), isotopically exchangeable phosphate (E) and the Larsen value (L) in a medium heavy loam treated with varying quantities of soluble phosphate.

situation is very different when widely contrasting soils are used, as is shown by the experiment for which results are given in Figure 3. There is then no consistent relationship between either the exchangeable soil phosphate or the "Larsen" value and the quantity of phosphate which the plants absorb. Over the whole series, however, absorption is clearly related to the reciprocal of the quantity of phosphate the soils sorb or remove from the solution under standard conditions. This result is compatible with the view that it is the potential of a nutrient which determines absorption by plants, for the quantity of phosphate sorbed by each soil in the series is inversely related to the concentration left in the soil solution, in other words, to the potential. The good agreement between the quantity of ions in the labile pool and the extent of absorption by plants observed in soils of similar type (Figure 2) is thus regarded as

an indirect relationship; it reflects the fact that, in closely similar soils, the relationship between the potential and the capacity of the labile pool is relatively constant.

The significance of the potential and the capacity of the labile nutrient pool may be illustrated by a simple analogy. If two tanks contain the same amount of water, but the surface area of one is half that of the other, the pressure in a pipe leading from the bottom of the narrow tank will be twice as great because of the greater depth of water. The greater pressure or potential of water in the tap from the narrow tank will cause more rapid flow. The quantity of water in the tank (or in the labile pool) is the same in both cases, but the rate at which water comes out of the tap (or nutrients enter plants) is greater when the potential is high.

This analogy reveals another point. If equal additions of water are made to both tanks there will be a larger increase in pressure in the pipe from the narrower tank. Similarly the addition of a given quantity of a nutrient to the soil is likely to bring about the largest increase in absorption by plants if the quantity of phosphate in the labile pool is small relative to the potential. The analogy also provides an interpretation of the well-known phenomena of phosphate "fixation." In soils where this occurs the addition of phosphate causes little increase in the absorption by plants, even though some residual effect of the added phosphate may remain over long periods. In such soils the relationship between the potential of the labile pool and its total size is low; those at the right-hand side of the series in Figure 3 were of this type. Despite its small effect, however, the phosphate added to such soils is not lost; it remains in the labile pool (or in the tank). It should therefore not be regarded as "fixed" and useless but rather as a capital investment; its presence will enable the next addition to increase the potential to a greater extent than would otherwise occur. The potential of the major plant nutrients other than phosphate does not seem to be lowered either to such a variable or such a large extent, but it appears that the same principles apply.

This description is of course a simplification of the situation that occurs in the complex medium of natural soils. For example, reactions take place between the readily exchangeable ions and sparingly soluble forms, and some nutrients may revert to very slowly soluble forms. None the less the key to soil/plant relationships appears to lie mainly in the behaviour of the labile nutrient pool.

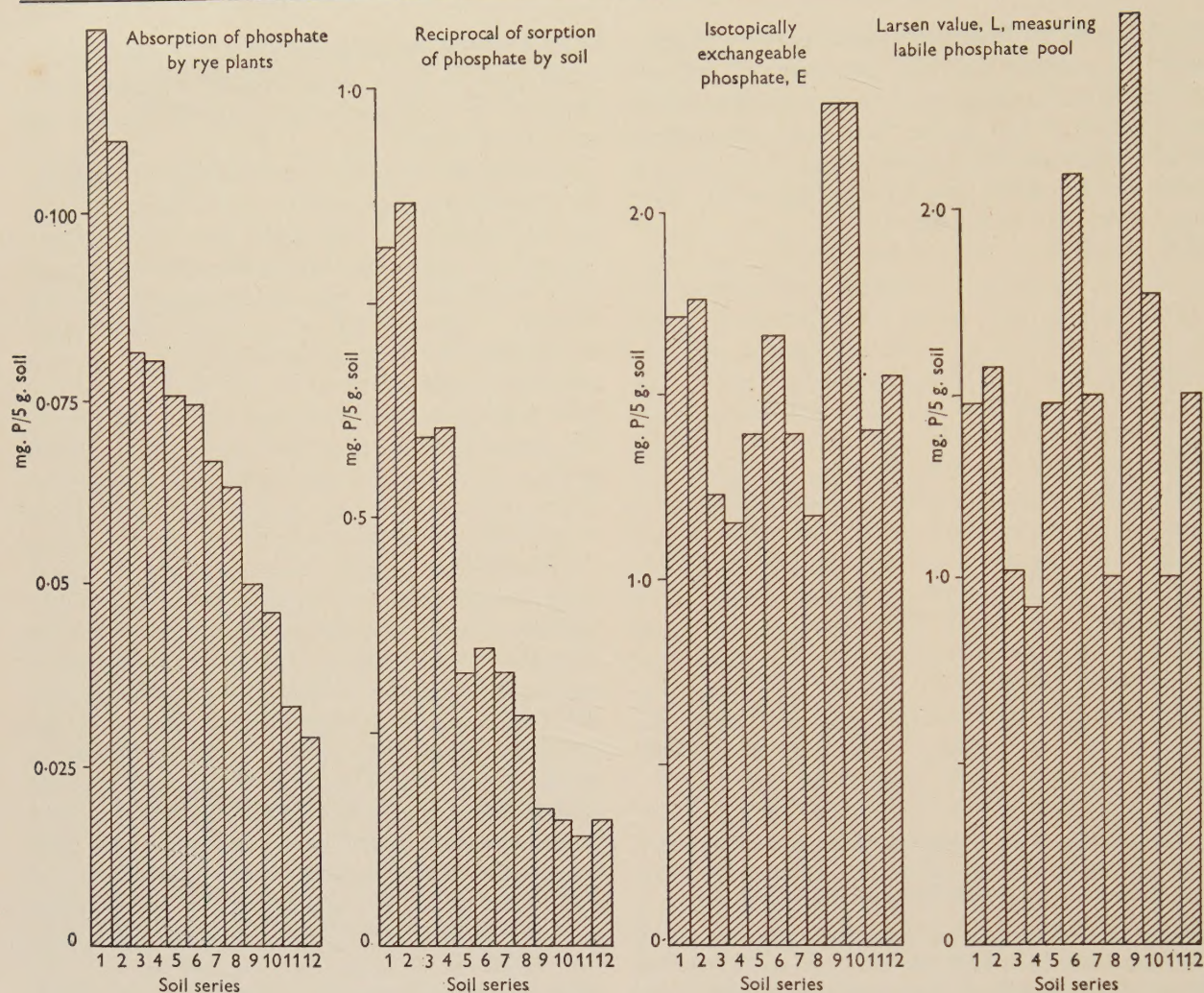


FIG. 3. Absorption of phosphate by rye plants from contrasting soils containing added phosphate compared with phosphate potential (measured by reciprocal of sorption of phosphate by soil), and with labile phosphate pool (measured by isotopically exchangeable phosphate and by Larsen value).

Many factors, controlled by climate or the management of land, can modify the capacity or the potential of the labile pool. As an example the effect of a change in the acidity of the soil may be considered. The addition of lime increases the pH of the soil and renders iron and manganese and other nutrients less soluble; decreasing pH, which may be brought about by bad fertilizer practice, waterlogging and other causes, may on the other hand reduce the potential of phosphate. Figure 4 illustrates some general relationships between the soil's acidity (pH) and the availability of nutrients to plants [20].

In some circumstances micro-organisms may influence the size of the labile nutrient pool. They bring about the mineralization of nutrients, especially during the decomposition of organic matter,

and they can control the oxidation and reduction of some inorganic nutrient elements, such as nitrogen, sulphur, iron and manganese. On the other hand, the quantity of nutrients in the labile pool may be temporarily reduced by absorption into microbial tissues, especially when the micro-organisms are stimulated to great activity by the addition of energy-rich organic matter to the soil [12]. It has long been known that there is a marked increase in microbial activity at the surface of roots, the volume of soil in which this population lives being called the rhizosphere. The accumulation of carbon dioxide produced by the micro-organisms in this volume of soil may influence the pH around the plant root and so affect the availability of nutrients in the manner illustrated by Figure 4, but the influence of the

rhizosphere on nutrient availability is still little understood. Mycorrhiza, the symbiotic association between fungi and roots, especially of trees, may also influence the characteristics of the labile pool; but these relationships are again imperfectly understood. It is, however, established that, despite the importance of micro-organisms in soil, organic media are not essential for the growth of plants;

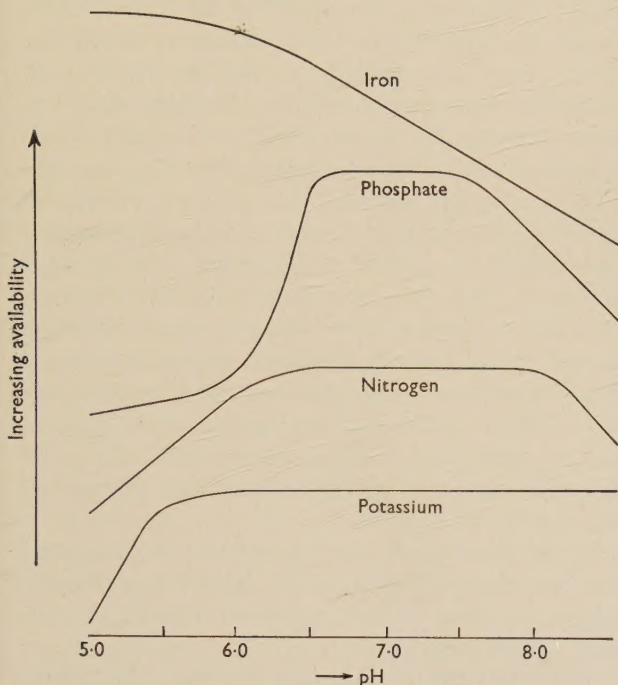


FIG. 4. Effect of soil acidity on the availability of nutrients to plants. (The relative availability of the different nutrients cannot be inferred from the curves.)

an adequate supply of mineral salts only can lead to optimal growth.

The extent to which nutrients move in soils is of considerable importance. Fertilizers are frequently applied in the form of granules irregularly distributed through the soil, and plant roots deplete the labile pool mainly at relatively limited sites, so that the level at which the supply to plants is maintained may be greatly influenced by the rate at which the nutrients move. Two types of mechanism enable ions to pass through the soil, namely mass movement in water and diffusion in exchange complexes; observations under constant conditions show that the rate of mass movement in water is directly proportional to time, whereas the extent of diffusion is proportional to the square root of time and so becomes progressively less as time passes. The rate at which ions penetrate the soil depends largely on the extent to which they are

held, through exchange and other reactions, on soil surfaces. Ions not held in this way, for example, nitrate, move largely by mass flow in water. There is evidence however that the redistribution of relatively immobile ions, such as phosphate and calcium, is due largely to diffusion.

THE MODE OF ENTRY OF NUTRIENTS INTO PLANT ROOTS

Most of our knowledge of the processes by which plants accumulate nutrients has been obtained from experiments using solution culture techniques. Quantitative experiments can be far more easily carried out by these methods, and complications that occur in the soil, such as the interaction between ions in a liquid and in a solid phase, are eliminated. Nutrients enter plants as dissociated ions in solution and, all other factors being equal, the accumulation of monovalent ions exceeds that of divalents, although many factors, some of which are referred to later, affect such relationships.

One of the important steps in our understanding of the mechanism of nutrient absorption was the discovery that it is an active process dependent on the use of energy released by respiration. Investigations initiated by Steward and Hoagland in California [7, 18] showed that the accumulation of ions in tissues varied with temperature, with the supply of oxygen and with the availability of respirable material, in much the same way as respiration. More recently it has been shown that the concentration of ions in plant sap may greatly exceed that in the outer medium, sometimes by factors exceeding 100 [4, 15]. Such concentration differences could only be brought about by the expenditure of energy.

Nevertheless, even within a single plant cell, the nature of the mechanism responsible for the accumulation of ions is far from clear, and in intact plants the situation is still more complex. In considering the latter subject it is necessary to have in mind the anatomy of the root through which ions are absorbed. The structure of the root a few millimetres behind the growing apex is of particular interest, for absorption has been shown to be most marked in this region [19]. Three zones of tissue are to be distinguished (Figure 5): a central conducting strand or vascular stele; a single layer of closely packed cells, the endodermis, surrounding the stele; and, external to this, the loosely packed parenchymatous cells of the cortex bounded by the epidermis. Root hairs are developed as extensions

from the epidermis in the young root and it has been suggested that they are the major sites of nutrient entry, but this has not been conclusively demonstrated. Ions on their way from the exterior of plant roots to the shoots must enter the root cortex, pass to the xylem, and move upward in the xylem to the shoot. At any point, however, they may be retained temporarily or permanently in

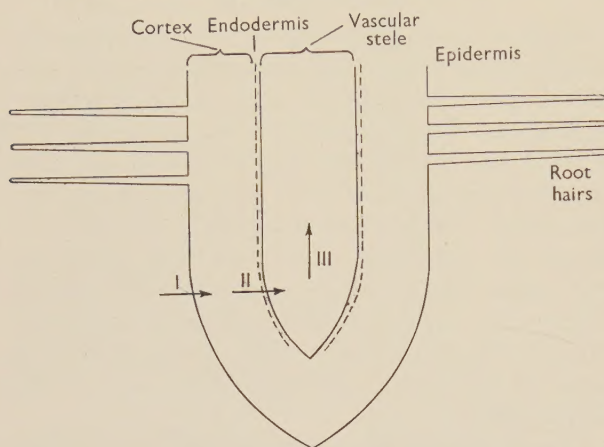


FIG. 5. Diagram of a longitudinal section of a root tip, illustrating the three main stages of nutrient absorption.

cells. Processes analogous to those involved in the first two stages occur when ions enter a single cell, but the initial entry is into the cytoplasm and transference is to the vacuole.

Experiments with root systems, slices of tissue and also algae show that absorption has two phases. When such tissues are transferred to a solution of salts a rapid initial influx of ions is followed by a slower and much more prolonged absorption. Although the relation between these two phases of uptake and the sites at which they occur is still a matter of debate, it is known that whereas the slower prolonged phase is closely linked with the use of respiratory energy the initial rapid uptake shows largely, though not entirely, the characteristics of a simple physical process. It still continues at low temperatures (e.g. 0.2°C) or in the presence of metabolic inhibitors although both of these conditions inhibit the release of energy through respiration. Cations are absorbed to a considerably greater extent than anions in the initial process.

Our understanding of the initial flux of ions has been greatly aided by the concept of "apparent free space" formulated by Briggs [1]. The "free space" is the volume of the tissue which ions can enter readily by processes of diffusion and ionic

exchange. Two components of the apparent free space have been recognized, namely "water free space" and "Donnan free space" [2]. Water free space has been regarded as the volume of available intercellular water in which ions attain the same concentration as in the exterior; in "Donnan free space" accumulation is brought about by the fixed charges on molecules adjacent to the aqueous phase. It is widely agreed that the initial rapid phase of absorption is due to ions entering the "free space," the location of which, however, is uncertain. Some workers have concluded that free space extends through a considerable part of the cytoplasm, while others suggest that it is confined to the cell walls and the intercellular spaces [5]. Although the extent to which free space penetrates the cortical tissues of intact roots remains unknown, it is apparent that it does not extend across the entire symplast of the root to the conducting tissues. The existence of a high resistance barrier across which ions must be actively transported is shown both by the effect of respiratory inhibitors and by the fact that the concentration of ions in the xylem sap may greatly exceed that external to the root [4, 11, 15].

There is as yet no agreement as to the nature of the "ion pump" which brings about the process of active transport. Many types of "carrier mechanism" have been postulated. The majority share the common assumption that the ion is bound by a product of metabolism at the exterior of a barrier which would offer a high resistance to the passage of free ions, and that in consequence of the expenditure of metabolic energy the ion is released at the interior. No detailed explanation of the nature of the "pump" can perhaps be expected until the complex molecular orientation of cytoplasmic membranes is understood. The weight of present evidence suggests that the endodermis is the site of the high resistance barrier across which ions are transferred by metabolic energy during their entry into plant roots, though there is no direct experimental evidence to prove this. The anatomical peculiarities of this tissue are, however, suggestive of a special function: it is a single layer of cells lacking intercellular spaces; the Casparian strip (a band of thickening) occurs on the cell walls; it contrasts sharply with the cortical tissues not only in these characteristics but also in having densely packed cytoplasm.

The onward passage to the plant shoot of ions that have been released into the conducting tissue appears to be due to a passive process of diffusion.

The rate of water movement, that is to say the rate of transpiration, thus has a great effect on the upward transfer of these ions. Yet a simple relationship is rarely apparent between transpiration and the rate at which nutrients are transferred from the exterior of roots to plant shoots.

The rate of the overall process will be determined by whichever of the three stages of entry is rate limiting under the existing conditions. In practice it is found that the movement of ions to plant shoots varies closely with the rate of transpiration when the external ionic concentration and the nutrient content of the tissues are both high [15]; but when the external ionic concentration is low wide variations in the rate of transpiration may have little or no effect. This view, first expressed by Broyer and Hoagland [3], is considered to be supported by much recent data [15]: when the external concentration is low the rate of transfer through the plant is controlled by the quantity of ions that is actively transported, thus variations in the rate of transpiration are without effect; if, however, the active transport system is sufficiently saturated the rate at which ions are removed from the interior of the root to the shoot becomes rate limiting, so that increased removal, effected by enhanced transpiration, accelerates transport.

FACTORS AFFECTING THE RATE AT WHICH NUTRIENTS ARE ABSORBED BY PLANTS

The importance of temperature, water supply and aeration of the rooting medium has been indicated in the foregoing discussion of the mechanism of nutrient absorption. In some plant species, however, the need for well aerated soil is markedly reduced on account of the development of an aerenchyma, of loosely packed cortical cells, in which oxygen can diffuse down to the roots from the aerial parts. Plants adapted to growth in waterlogged situations may show this characteristic.

The concentration of nutrients both outside and inside the plant is a major factor in determining the rate of absorption. If the external supply is sufficiently low, absorption is usually proportional to the external concentration, so that an increase in the nutrient supply causes a corresponding increase in absorption. But the increments in uptake decrease progressively as the supply becomes greater until a point is reached at which there is little additional effect. The law of diminishing returns thus operates and, in consequence, the

fertilizer dressing that gives the maximum yield may not give the maximum profit. The effect of the internal concentration on absorption is the reverse of that of the external supply. Plants that contain a nutrient in low concentration will, in general, absorb it more freely; this principle provides an explanation of the effect of the use made of nutrients on their absorption. In an actively growing plant the internal concentration of ions is largely determined by the rate at which they are used in metabolic processes. For example, if nitrate and phosphate are being rapidly metabolized into organic compounds, their internal ionic concentration remains low and absorption is therefore accelerated. In contrast, the concentration of an ion that does not enter into metabolism, such as chloride, will increase within the tissue and the extent to which it is absorbed will be reduced. The net effect is that the nutritional requirements of the plant for growth largely determine the rates at which different ions enter, assuming that the external supply is ample. Plants therefore appear to select the nutrients they require for growth, although in fact there is no positive mechanism of selection. If the concentration, valency and size of ions are such that the ions can enter the plant they will be absorbed even though their presence is unnecessary, or even injurious.

Interactions between different ions have far-reaching effects and may be brought about by many contrasting types of mechanism. The simplest type of ionic interaction is competition between ions of the same sign in the absorption process. Thus, by increasing the concentration of any one cation the rate of entry of other cations usually tends to be reduced: application of excessive dressings of one nutrient may therefore lead to deficiency of another [22]. Interactions may also occur within plants, for example an excessive absorption of iron may cause phosphate to be bound in complex forms in plants [6]. On the other hand the enhanced absorption of one nutrient may accelerate the absorption of another; an example from laboratory experiments is that the presence of calcium in a solution may increase the absorption of other cations, apparently owing to the effect of calcium on cytoplasmic mechanisms [21]. In the field, however, this phenomenon is due chiefly to an increase in the capacity of the plant to use nutrients; if phosphate is given to plants deficient of that element, their absorption of nutrients and particularly nitrogen, may be increased because the more favourable supply of phosphate

hastens metabolic processes. In all these interactions an exact electrostatic balance is always maintained between the net entry of anions and of cations.

The influence of the rate of plant growth, though indirect, is such that the pattern of nutrient absorption will change progressively with that of growth throughout the life-cycle of a plant. This is

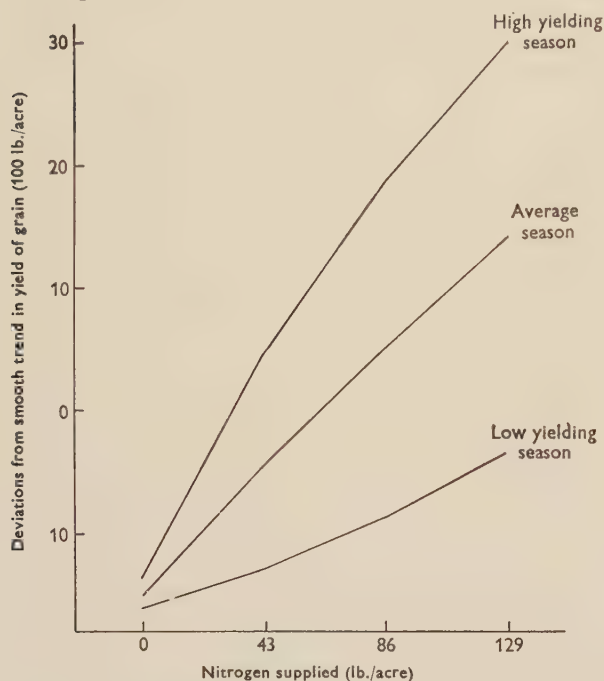


FIG. 6. Relationship between yield of grain and nitrogen supply at different levels of mean yield.

marked in crops like cereals which have a complex pattern of development: in their early stages, when rapid vegetative expansion occurs, the absorption of nutrients, especially of potassium, is maximal; later, when the volume of actively metabolizing tissue is reduced by the death of old leaves and infertile tillers, not only may the absorption of potassium cease but an appreciable loss from the plant may occur [23].

Climate largely has an indirect effect, absorption being greatest when the conditions are most favourable for the intake and use of nutrients. An excellent instance is to be found in the long series of experiments with wheat at Rothamsted, which show that fertilizers have their greatest effect in years when the average level of yield is high [13] (Figure 6).

It may be said, therefore, that every factor of the environment that affects plant growth will influence the rate at which nutrients are absorbed, either directly by influencing the mechanism of entry or indirectly by altering the rate of growth. Further, the entry of an ion into the plant is not to be considered in isolation; account must be taken of the ratios in which ions are supplied as well as of their individual concentrations.

Because of the complexity of these relationships and variability in climatic conditions it is not surprising that, despite more than a century of research, the exact benefit that will accrue each season from the application of fertilizers cannot be predicted.

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FOLIAR APPLICATION OF MAJOR NUTRIENTS TO FRUIT AND PLANTATION CROPS

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Possible advantages of foliar application of nutrients—in efficiency, speed, cheapness, and effect on crop quality—have attracted attention for many years. Progress has been most rapid for fruit and plantation crops, especially in the last decade; but the promise of foliar application of nutrients and the risk of injury to the foliage may be appraised only by the study of individual crops, as is done in the present review.

It has long been known that plants are capable of absorbing nutrients through their leaves. Research on this subject has been greatly stimulated in recent years by the use of radioactive isotopes, by the availability of concentrated highly soluble fertilizers and by the development of suitable sprayers.

Some of the earliest references to foliar nutrition are from France and Germany [16, 33, 36, 49]. Reviews of the literature have been made by various workers [19, 44, 69, 70, 76, 77].

Efficiency of nutrient uptake from foliar sprays may be expected to be greatest, in comparison with that from solid fertilizers applied to the soil, when special limitations exist. Such conditions may occur, for example, when nutrients are rapidly "fixed" by the soil in a form that is not readily available to plants, or where there is competition for soil nutrients from weeds, ground cover (e.g. grass in a grassed-down orchard) or shade plants. Although a foliar spray can be applied selectively to the crop alone, it does not necessarily follow that any increase in efficiency of uptake from foliar application will result in a corresponding increase in crop yield.

Sometimes, when the crop is at a late stage of growth, the only practicable methods of fertilizer application may be spraying or dusting, and here the use of a foliar spray, whether from the ground or from the air, may have special advantages.

The speed of uptake of nutrients from foliar sprays may well be decisive in an emergency. Deficiencies may be corrected at the earliest visible or detectable stage, and in some cases serious crop losses may be avoided. On the other hand, rain falling shortly after application may wash a foliar spray into the soil with loss of any advantage inherent in spraying, or run-off from the spray itself may result in some leaching of nutrients from the leaves. The effects of soil application, though slower to be realized, may be longer lasting.

Changes in plant composition resulting from nutrient sprays can, under certain circumstances, affect susceptibility or resistance to disease and also the quality and nutritional value of the harvested crop. Cereals have been sprayed at the time of earing to secure grain of enhanced protein content.

Where there is a regular spraying programme for pesticides on fruit crops it may be possible to incorporate soluble fertilizer nutrients in the sprays at a cost scarcely higher than that of the chemicals. Where a contract spraying service is available, therefore, a foliar spray might be applied more cheaply than a solid fertilizer. In general, however, a number of factors tend to make spraying more costly, among them being the limitations imposed by the maximum volume of liquid that can be retained on the leaf surfaces, the risk of leaf scorch if the concentration of nutrients in the spray exceeds a certain level, and the generally greater cost of the more highly soluble fertilizer materials.

Since phosphorus is so easily "fixed" by the soil in a form that is only slowly available to plants, one would expect foliar application of this nutrient to be more efficient than application to the soil. In practice there has been greater commercial interest in nitrogen than in phosphate, partly on account of the relative costs of the materials used and partly, perhaps, because many crops need an ample supply of easily available phosphorus early in the season when the leaf area is too small to retain much spray. Nitrogen, too, is required early, but it is quite common for a basal dressing to be followed by one or more topdressings which might be replaced by foliar sprays.

CHOICE OF CHEMICAL

Most nitrogenous fertilizers are readily soluble in water, and experiments have been reported with foliar sprays of solutions of nitrates, ammonium compounds, cyanamides and urea. Interest has

centred on urea on account of its high nitrogen content, high degree of solubility, and lack of corrosiveness to metals. Urea is absorbed, transported and metabolized as rapidly as any nutrient applied to plant foliage, and the risk of scorching is usually less than with sprays supplying equivalent quantities of nitrogen in other forms. The concentration employed for high-volume application on fruit crops, such as apples, is usually about 5 lb. urea per 100 gallons of water. For low-volume, mist application, 10 lb. urea may be given in 20 gal./acre. On some of the less sensitive agricultural crops, such as cereals and grasses, or for application from aircraft, even higher concentrations may be used. At Jealott's Hill [46], for example, a solution of 88 lb. urea in 13.4 gallons of water, giving 20 gallons of solution, was applied at 20 gal./acre to an Italian ryegrass sward with a good response in terms of dry weight and crude protein and little or no damage to the herbage.

Many phosphorus compounds have been studied, but none is so pre-eminently suited to foliar nutrition as is urea among chemicals supplying nitrogen. Orthophosphoric acid, calcium glycerophosphate, di-ammonium phosphate and mono- and di-potassium phosphates have all been used with modest success at concentrations supplying about 0.1–0.2% P_2O_5 , as have indeed a number of other phosphates, including superphosphate.

The sulphate is probably the most satisfactory potassium source for foliar application but may cause some leaf scorch when applied in 1% solution. The chloride, citrate and nitrate have also been used with success.

Although there is evidence that magnesium chloride and nitrate are more rapidly taken up than the sulphate, they are also more liable to cause damage. A solution of 20 lb. Epsom salts ($MgSO_4 \cdot 7H_2O$) in 100 gallons of water is recommended for foliar application to many crops.

RESULTS WITH FRUIT CROPS

Apples. Accurate control of nitrogen nutrition is probably more important for yield and quality in apples than in any other fruit crop. Experiments in New York State [34] to determine the effect of various nitrogenous substances applied with the regular scab sulphur sprays showed that urea at 5 lb./100 gal. caused no apparent injury to the foliage and produced a very rapid increase in the green colour of the leaves. Sodium nitrate, potassium nitrate and ammonium nitrate at 5 lb./100 gal. caused considerable leaf scorch, as did

urea at 10–20 lb./100 gal. The combination of 5 lb. urea/100 gal. with sulphur and lead arsenate resulted in less scab than when a similar amount of nitrogen was applied to the soil at the beginning of the year. In a long-term study [60] Cornell University investigators have found that including urea at 5 lb./100 gal. in the first three pesticidal sprays after blossoming is sufficient to maintain a satisfactory nitrogen level in an orchard of moderate vigour. Early applications before the June drop result in greater fruit set and better colour, and later applications in greater fruit size and probably poorer colour, depending on the lateness of maturity. A combination of soil application of urea at $1\frac{1}{2}$ lb./tree and three post-blossom foliage sprays at 3 lb./100 gal. is suggested as a satisfactory commercial practice.

In Vermont [15], 3 or 4 applications per year of 5 lb. urea/100 gal. (15 gal./tree at each application) produced large increases in yield as more spurs matured two or three apples instead of only one; but the fruit tended to be less firm and to contain fewer solids.

In Washington State [14] satisfactory results have been obtained by 2–3 sprayings of 5 lb. urea/100 gal. annually to give 70 lb. N/acre, with the proviso that applications after 25th June should be avoided in order not to delay maturity and colouring of fruit. Aircraft application of a concentrated solution of 70 lb. urea/10 gal. water has been made successfully under various weather conditions without causing damage to the foliage.

In S.W. England [66], spraying with 5 lb. urea/100 gal. (300–400 gal./acre) at green cluster, pink bud and petal fall stages gave better leaf growth and colour throughout the summer, and noticeably improved the quality and size of the fruit. Addition of urea to routine lime sulphur sprays did not scorch the leaves if no other salt, such as magnesium or manganese sulphate, was added at the same time.

At Long Ashton [17, 71] spraying urea at petal fall was most effective in maintaining a dark green leaf colour under conditions where soil application of a nitrogenous fertilizer appeared to stimulate only the grass cover crop.

Laboratory and greenhouse investigations have shown that absorption of urea by the leaves is most rapid during the first few hours after spraying but continues for at least 48 hours. Absorption is more rapid in younger than in older leaves.

Orthophosphoric acid and diammonium phosphate sprays have given the most rapid intake and

translocation of phosphate, but absorption was continuous over at least 30 days from spraying and the sprays were unable to provide for the total phosphate requirements of the trees [30].

Potassium deficiency has been corrected by repeated spraying with 1% solution of potassium sulphate but not without some leaf injury [24, 25]. The spray should be applied after blossoming.

Magnesium deficiency symptoms can be suppressed by spraying 3–4 times at fortnightly intervals from petal fall with Epsom salts (20 lb./100 gal.) or calcined kieserite solution [18]. This treatment is effective in the year in which it is applied, whereas soil applications may not become effective for 2 or 3 years, particularly in grassed orchards. Foliar sprays, on the other hand, have little or no residual effect.

Pears. Urea sprays (5 lb./100 gal.) have been used on pears without causing leaf damage but without any marked benefit [66].

Cherries. Foliar sprays of sodium nitrate, potassium nitrate, ammonium nitrate, ammonium sulphate and urea at 5 lb./100 gal. have been used without causing leaf injury, but again without any significant improvement in growth, yield or quality [34]. Urea containing over 0.5% biuret was harmful, leaf injury increasing progressively with the proportion of biuret [73].

Apricots and Plums. Little benefit has been obtained from urea sprays (5 lb./100 gal.) under conditions where soil application gave normal improvement [61, 62].

Peaches. In the greenhouse peach leaves absorb and utilize nitrogen from a urea spray, though less efficiently than apple leaves [59]. Field tests, however, have given disappointing results [61, 62, 75]. Repeated sprayings of urea at 5 lb./100 gal., while not causing leaf injury, have generally failed to produce any satisfactory response. Higher concentrations were no more effective and caused some marginal burning of the leaves and slight defoliation.

Citrus fruits. Urea is readily absorbed by the foliage, more rapidly by orange than by lemon and by younger than by older leaves [45]. Spraying with urea has been widely practised on commercial orchards in California. "Yellow tip" on Valencia orange leaves was shown to result from too high a proportion of biuret [42].

Magnesium deficiency in citrus as in apple trees can be effectively controlled by foliar sprays of Epsom salts (20 lb./100 gal.).

Figs and Olives. There are indications that urea

sprays at 5 lb./100 gal. may have possibilities for figs and olives [61–63].

Walnuts and Almonds. Severe injury to walnuts followed a foliar spray of 10 lb. urea/100 gal. [61, 62]. Almonds have been damaged at half the strength [59].

Grapes. Results with urea are variable. Leaf injury was avoided by adding copper in the form of Bordeaux mixture to sprays containing up to 4 lb. urea/100 gal. [47]. Urea spraying may possibly affect the sugar content of the grapes and must [28, 29, 37].

Magnesium deficiency may be controlled by two or more sprays of Epsom salts (20–40 lb./100 gal.). The effects of spraying are visible after six weeks, while soil applications may not become effective for a year or more. Magnesium nitrate and chloride were more rapidly taken up than other compounds, but at the equivalent of 40 lb. Epsom salts/100 gal. both caused some leaf damage [35, 68].

Blackcurrants. Very encouraging results have been obtained by spraying with 20 lb. urea/100 gal. under conditions where it had been found difficult to correct nitrogen deficiency caused by excessive mulching with sawdust. No damage resulted and there was considerably less leaf spot caused by *Pseudopeziza ribis* on the treated bushes, possibly because of the lowered K/N ratio [66]. A 2% solution of superphosphate has proved a satisfactory source of phosphate [39, 40].

Gooseberries. Gooseberry bushes grown under conditions of acute potassium deficiency absorb enough of this element through their leaves from a 1% solution of potassium sulphate to prevent development of leaf scorch [74]. Recent investigations failed to show any benefit from spraying with urea at 5 lb./100 gal. [1].

RESULTS WITH PLANTATION CROPS

Bananas. Absorption of nitrogen from urea foliar sprays is particularly rapid; as much as 65% was absorbed within 25 minutes under humid conditions in the greenhouse. Even under dry conditions 62% was absorbed in 24 hours. The spray used in these experiments was a 0.75% urea solution, with or without Bordeaux [32]. In another experiment with a 3.3% urea solution absorption was virtually complete in 30 hours [26].

Pineapples. In Queensland [2, 27] good results have been obtained by applying urea at 1 lb./gal. (30–50 gal./acre) once every two months. In East

Africa [31, 41] a 5% concentration is considered safe during the dry season, though much stronger solutions can be used during the wet season. Urea sprays are possibly not quite so effective as soil applications of ammonium sulphate at equivalent rates per acre. 2% magnesium sulphate sprayed five times at monthly intervals produced a significant increase in mean fruit weight though not in yield per acre.

Sugarcane. Experience in Hawaii and elsewhere has shown that urea is quickly absorbed by the leaves, though the resultant cane yield is not necessarily any higher than from solid fertilizer application. A single spraying from aircraft with saturated urea solution has proved an effective method of giving additional nitrogen after the cane has closed in. The crop was uninjured provided the plants were high in moisture at the time. Aerial spraying of 28½% potassium chloride solution at 10 gal./acre has also been successful at a late stage of growth; but phosphate enters the plant more slowly and is best applied in solid form at planting time [21–3, 38].

Tea. Foliar spraying of ammonium sulphate has been studied at Tocklai [3, 4], using concentrations from 0.1% to 5.0%. Concentrations over 1% were unsafe. In Ceylon [55] spraying with 6% urea solution 2–4 times at weekly intervals removed pink leaf symptoms but caused slight scorching. There was no scorching with 3% urea solution. In South India spraying of 1% potassium chloride in four rounds at 4–5 day intervals in December/January and again in April, to give an annual rate of 53 lb. K₂O/acre, substantially increased yield of green leaf [5–7, 72]. The additional response to nitrogen and phosphate—1¼% urea and 1% superphosphate in the spray, providing annually a total of 50 lb. N and 15 lb. P₂O₅/acre—was not significant. In Ceylon [56] spraying with 10% solution of Epsom salts over an

eight-week period effectively controlled magnesium deficiency. Spraying with less concentrated solutions over a longer period was not quite so effective.

Coffee. Although laboratory studies [26] indicate a rapid absorption of urea by coffee leaves, virtually complete within 24 hours, field trials have given variable results. In South India [8, 9] foliar application of urea and potassium chloride to provide 20 and 40 lb. each of N and K₂O per acre, failed to produce a significant response. In one experiment in Brazil there was an unsatisfactory response to urea sprays at 0.8, 1.76 and 2.64% N, but in another experiment three sprays of 2.5% urea at fortnightly intervals raised the leaf content of N-deficient plants and produced a deeper green leaf coloration than application of nitrogenous fertilizer to the soil [50–2, 54]. In Kenya [43, 67] it is recommended that to avoid leaf scorch the strength of urea should not exceed 1% in medium and high volume sprays and that biuret, if present, should not exceed 1% by weight in the urea. Where higher concentrations are used the biuret content of the urea should be below 0.5%. Unsuccessful magnesium spraying has been reported from Uganda [10].

Cacao. Excellent results have been obtained in Colombia [48, 53, 57, 58] by spraying with urea (0.5 or 1.0%), calcium glycerophosphate and potassium chloride either before or after pollination. If combined with routine pesticidal spraying, the treatment is cheaper than soil application of fertilizers. Unsatisfactory results reported from Costa Rica [20] were attributed to lack of active growth of the cacao seedlings at the time of spraying.

Tobacco. Experiments in various parts of the world [11, 12, 13, 64, 65] have shown that tobacco is capable of absorbing all three major plant nutrients from foliar sprays; some increases in yield have been reported.

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THE FRUIT FLY PROBLEM IN AUSTRALIA

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Fruit flies causing blemishes and destruction are serious pests of pome and stone fruits. The indigenous Queensland fruit fly is still spreading, in spite of energetic control measures; eradication is considered impracticable, but containment may be achieved. The introduced Mediterranean fruit fly is being held in check by present remedies and ecological barriers; there is some hope that Australia may eventually be rid of it.

Certain members of the fruit fly family (*Trypetidae*) whether indigenous or introduced, are regarded as the most destructive pests of fruit in many areas of the world. In Australia, two species of fruit fly, the Queensland fruit fly (*Strumeta tryoni* (Frogg.)) (Figure 2) and the Mediterranean fruit fly (*Ceratitis capitata* (Wied.)), cause very considerable economic loss. The female fly usually selects ripe or ripening fruit for oviposition, and small groups of eggs, normally five to nine in number, are laid just beneath the punctures or "stings" in the skin of the fruit (Figure 1). The resulting larvae feed throughout the tissue of the fruit, destroying much of it and facilitating decomposition (Figure 3). The damaged fruit may drop prematurely; it is always unmarketable. In general, the areas in which fruit fly attack occurs are restricted to the warmer parts of the continent, although from time to time outbreaks have occurred in cooler districts in the south.

S. tryoni, a native insect, first recorded in Queensland about 100 years ago, has extended its range and is now well established in Queensland and coastal New South Wales, and to a lesser extent in Victoria near the southern limit of the continent. *C. capitata*, the only introduced fruit fly to become established in Australia, was reported in New South Wales, Victoria and Western Australia by the early 1900s but is now restricted to Western Australia [2, 8].

A large number of indigenous fruit fly species breed in the fruits of native plants, and a few will also attack cultivated plants. *S. tryoni* is by far the most destructive, with a very wide host range including all cultivated fruits with the exception of pineapples, strawberries and cucurbits. In Queensland the cucumber fly (*Austrodacus cucumis* (French)) attacks cucurbits, tomatoes and pawpaws. Among associated but less important species, *Afrodacus jarvisi* (Tryon) attacks deciduous fruits and persimmons, *S. halfordiae* (Tryon) loquats and citrus, and *S. humeralis* (Perk.) tomatoes and citrus

[1, 13]. *S. musae* (Tryon), which has been recorded also in New Guinea [14], is an important pest of bananas in northern Queensland.

This review is confined to the Queensland and Mediterranean flies, against which most of the control and preventive work has been directed.

DISTRIBUTION

The Queensland fruit fly was first recorded as a pest of fruit in the Toowoomba district of Queensland in 1853 [14]. Subsequent records indicate that the species was common in fruit-growing areas in that State and in the coastal areas of northern New South Wales by 1900 (Figure 6). Since then it has become firmly established as far south as Bateman's Bay in New South Wales and also to a lesser degree in the East Gippsland area of Victoria; recently it has been found at Lord Howe Island, approximately 500 miles east of Sydney. Isolated outbreaks have occurred in urban and inland areas of New South Wales, Victoria and South Australia, where stringent eradication measures have been applied. These measures, unsuitable climatic conditions, or both, have prevented the fly from becoming permanently established in these areas [2, 9, 15].

The extent of distribution of the Queensland fruit fly in the northern areas of the continent is unknown, but it is thought that the area of infestation may continue around the North Queensland coast into the Northern Territory and even into the Kimberley area of Western Australia. Commercial orchards are scarce in these areas and settlements sparse. The fly may be present already or it may well spread, eventually, into climatically suitable areas.

Many workers consider that the Queensland fruit fly would not survive in areas south of the Murray river because of its inability to overwinter in the higher and colder regions such as the Stanthorpe district in Queensland. It has persisted in the East Gippsland area of Victoria, however,



FIG. 1. Queensland fruit flies ovipositing on an apple.



FIG. 2 Adult female of the Queensland fruit fly.



FIG. 3. An infested apple, showing larvae of the Queensland fruit fly.



FIG. 4. The egg parasite *Opius oophilus* ovipositing in a fruit-fly-infested banana.

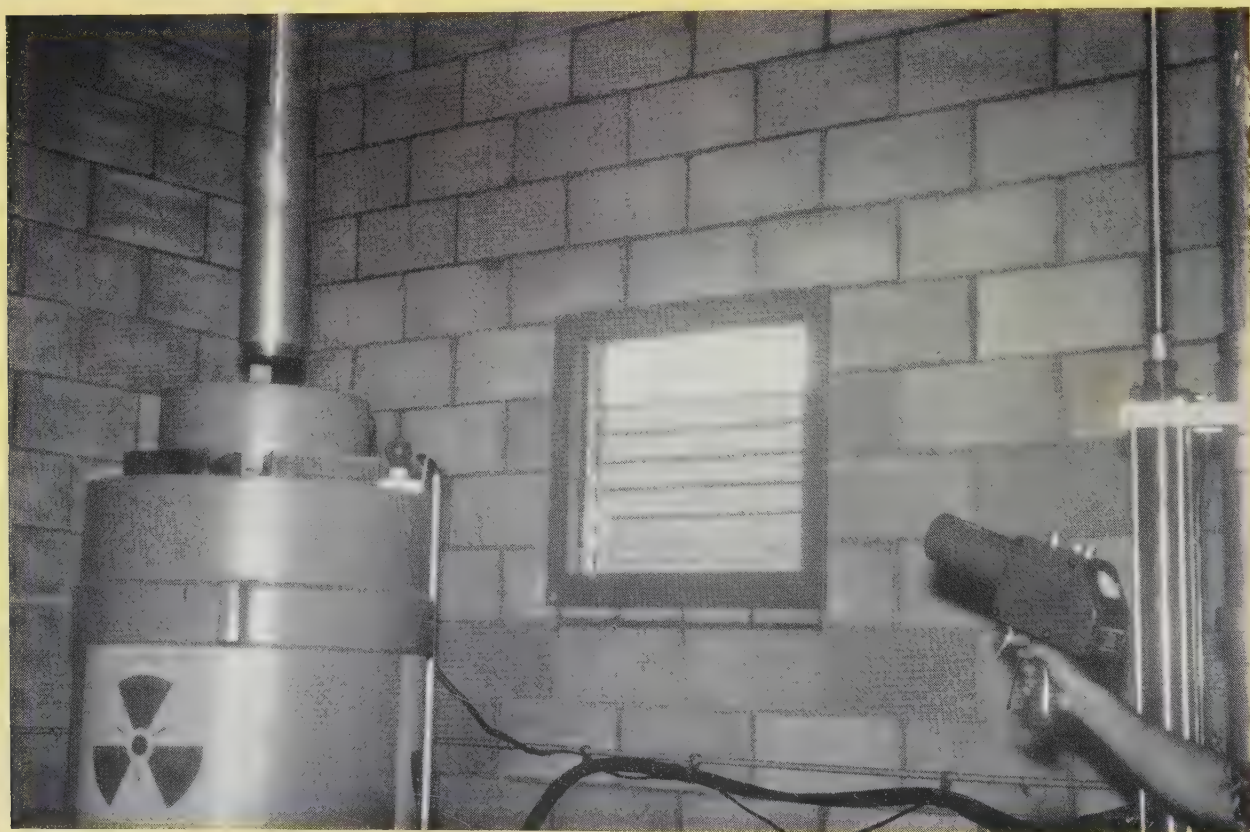


FIG. 5. A cylinder of *Dacus dorsalis* puparia being loaded into a Cobalt 60 unit for sterilisation in Hawaii.

since 1948, although the damage caused is less than in the warmer parts of Australia. Distinct varieties or geographic races may exist [6]. Whether a race will emerge capable of colonizing the southernmost parts of Australia, including Tasmania, remains to be seen; authorities are taking no chance of allowing this pest to become established.

The Mediterranean fruit fly was first recorded in Western Australia in 1897, and has become firmly established in the fruit-growing areas in the south-western portion of that State [9]. It is found permanently in an area bounded by Gingin in the north, Northam and York in the east, and Balingup and Busselton in the south. It has been found as far as Carnarvon in the north, Kalgoorlie in the east, and Albany in the south. Climatic conditions in the most southerly areas and the lack of continuity of suitable host plants in outlying districts probably restrict its permanent

establishment in these places [12]. This pest first appeared in Sydney in 1898, having been apparently introduced in a shipment of fruit from Western Australia. The fly quickly spread through the citrus-growing areas of New South Wales during the 1930s, but there are no records of infestation of fruit in that State since 1941 [2, 7, 14]. The reasons are obscure; some of the factors which could have influenced its disappearance and which might have operated singly or in combination are: food competition with the native Queensland fruit fly; unsuitable ecological or climatic conditions; and the adaptation of parasites of the indigenous fly to the new species.

Local outbreaks of the Mediterranean fruit fly have occurred over the last few years in both Victoria and South Australia, but vigorous eradication programmes have prevented the fly from becoming firmly established [2]. Outbreaks in



FIG. 6. Map of Australia, showing areas of infestation and isolated outbreaks of the Queensland and Mediterranean fruit flies.

northern Tasmania have not persisted for more than one or two years, probably owing to unfavourable climatic conditions [7].

The range of this fly outside the principal fruit and vegetable areas is probably limited only by the lack of suitable host plants. It tends to be replaced by the Queensland fruit fly whenever the two come into contact. Conceivably, in the absence of such competition, the Mediterranean fly would spread to all fruit-growing areas in the continent.

ECONOMIC IMPORTANCE

Although the Mediterranean fruit fly is regarded by authorities in many parts of the world as the most destructive pest of fruit, the Queensland fruit fly, where it occurs, is equally destructive; it appears to have a greater range of host fruits, and greatly restricts the varieties of fruit which can be grown. Subtropical as well as temperate fruits are attacked. The fly has caused many orchards to be abandoned in southern Queensland and coastal New South Wales, where, before 1900, large areas of pome and stone fruits were grown satisfactorily. Today these fruits are cultivated only in the cool highland areas where fruit flies are less active [16].

Costs of fruit production are considerably increased when compulsory measures must be taken against the pest. The grower must maintain regular cover or bait sprays during the ripening period and must also pick and destroy all infested and fallen fruit [2, 12, 15].

Indirectly, the greatest commercial losses from fruit flies are caused by restricting the markets to which produce can be sent. New Zealand, for example, will not accept fruit from any area where even a single fly has been found within the previous twelve months. This limitation causes greatest concern in extensive inland orchards, where the pest does not occur naturally but to which it might be carried unwittingly by travellers. When the regular overseas outlets fail, alternative local markets may become oversupplied, with consequent reduction in monetary return to the grower.

Quarantine measures have been adopted in the southern areas to limit the further spread of fruit flies; the cost of enforcing these regulations has been heavy. Restrictions on the free flow of produce into clean areas bring extra costs to the fruit industry. Should isolated outbreaks occur, eradication measures must be applied at once, and are expensive. The monetary losses attributable to the above factors are very large but cannot be definitely assessed.

BIOLOGICAL CONTROL

The introduction of parasites to combat both species of fruit fly has been tried over a period of years, but without striking results. Since successful biological control would be inexpensive, work along these lines continues. Although parasitic insects may be of some value against an introduced pest such as the Mediterranean fruit fly, it is extremely doubtful whether they can significantly reduce damage caused by the indigenous Queensland fruit fly. This insect has at least nine species of parasitic Braconids which seem to have had little, if any, effect on its numbers in commercial orchards [16].

The main work in biological control has been undertaken by the Commonwealth Scientific and Industrial Research Organization in New South Wales and Queensland, and as recently as 1959 a sub-station was set up in Hawaii in co-operation with the United States Department of Agriculture. There, many parasites, including the egg parasite *Opius oophilus* (Silv.), which had been instrumental in reducing populations of the Oriental fruit fly (*Dacus dorsalis* Hendel) in Hawaii, were bred up and subsequently introduced into Australia [4] (Figure 4). These parasites were liberated in both Eastern and Western Australia and specimens have been recaptured in the field, but their value under commercial growing conditions has yet to be assessed. In Eastern Australia, at least, they will have to compete with native parasites and adapt themselves to different ecological conditions. They will also be exposed in commercial orchards to chemical sprays normally used in the control of other pests—sprays which may be lethal to beneficial insects as well.

HYGIENE AND CHEMICAL CONTROL

Before the advent of DDT after the second world war, control measures against fruit flies in Australia were based on orchard hygiene and the use of lures and poison baits during the ripening of the fruit. Legislation was introduced in all states afflicted with the pests, requiring all persons with fruit trees in affected areas to bait regularly during ripening of the fruit, and to destroy all infested or fallen fruit by burning, boiling or burying. The baits mainly used contained tartar emetic or sodium fluosilicate and sugar, and were applied to small patches of the foliage every six or seven days from a spray machine, or splashed on with a brush. In Queensland, simple lure traps containing ammonia or

ammonium carbonate were hung in the orchard to detect fruit fly activity and to indicate when control measures should be undertaken [1, 2, 12].

When it was found that DDT sprays protected ripening fruit, recommendations in New South Wales and Queensland were amended to include the use of 0.2% DDT every seven to ten days as a cover spray [1, 2]. On deciduous fruit, however, DDT should not be applied within three weeks of harvest; bait sprays must be used during this period [5, 15]. In Western Australia, baiting with recommended materials has been preferred to cover spraying for the control of the Mediterranean fruit fly [13]. The use of DDT has the disadvantage of killing many natural and introduced enemies of fruit flies and of other pests which may therefore build up to such an extent that additional sprays are needed to combat them, as has happened with spider mites, scale insects, and many aphid species.

Several organo-phosphorus materials have also been tried as cover sprays for fruit fly control by a number of workers in this country. Some of these compounds, such as dipterex, Rogor and Lebaycid, which are capable of being absorbed into the fruit and of killing any larvae present, have been tried by orchardists. These materials appear to be more effective against the Mediterranean than against the Queensland fruit fly [5, 17]. In Western Australia they are recommended for use in commercial orchards and in home gardens, but in Queensland and New South Wales they are not used in commercial orchards except where fruit fly hazard is highest, for example, in blocks of stone-fruit trees in urban areas. In the same States, home gardeners, who may be inclined to overlook small blemishes from oviposition, have obtained better control of the Queensland fruit fly with these materials than by other methods.

With the invasion of the Oriental fruit fly into Hawaii during the second world war, research workers there evolved new methods of control based on earlier bait sprays. More effective attractants were found, such as protein hydrolysate, and from the large number of insecticides screened against fruit flies the phosphorus materials were preferred as stomach poisons. Malathion, which is relatively safe to humans and wildlife, was finally recommended. Hawaiian experience and methods were used in the eradication campaign against the Mediterranean fruit fly in Florida in 1956, the campaign being based largely on bait sprays containing malathion and protein hydro-

lysate. In Australia these materials were found to attract and kill both major species of fruit fly [5, 13]; but, as in Hawaii, bait sprays containing protein hydrolysate had limitations. Unless a large enough area could be treated, usually at least several acres, the degree of control was unsatisfactory. For home gardens, therefore, the method has been ineffective; for larger holdings or concentrated areas of fruit production, on the other hand, both in New South Wales and in Western Australia, it has been highly successful. It has not succeeded in Queensland, where climatic conditions probably affect the potency of the bait mixture, and where there is constant re-invasion from the surrounding countryside [16]. Mixtures containing malathion and protein hydrolysate have been officially recommended in both New South Wales and Western Australia and have also been used in several instances in other States as an eradication measure against isolated outbreaks [5, 13].

MALE SUPPRESSION AND STERILIZATION

The use of lure traps containing a chemical strongly attractive to the males and also a toxicant is being investigated in New South Wales [11]. Such traps have been used in isolated outbreaks to determine the success or otherwise of eradication measures applied.

No attempt has yet been made in Australia to control fruit flies by the release of male fruit flies sterilized by irradiation, but the method is being currently investigated for use against the Queensland fruit fly [11]. The procedure was employed in 1955 with great success by the United States Department of Agriculture for the control of screw worm in the West Indies.

While these two methods of control may be of value against the Mediterranean fruit fly in Western Australia and against isolated outbreaks of the Queensland fruit fly, it is extremely doubtful if they would be of any value against the latter in endemic areas, where the fly has such a wide range of native hosts outside commercial orchards; in addition, much of the large area concerned is inaccessible.

POST-HARVEST TREATMENTS

In the United States and other countries, treatment of infested produce after harvest has been approved by the authorities. When it became clear that the Queensland fruit fly, despite all measures taken against it, was spreading and

affecting both export and inter-State trade in fresh fruit, the Commonwealth Scientific and Industrial Research Organization and some Departments of Agriculture began to investigate the value of post-harvest treatments under Australian conditions. Low-temperature sterilization was found to be effective in killing all stages of the Queensland fruit fly. New Zealand now accepts oranges from areas affected by the Queensland fruit fly provided the fruit has first been stored at 31° F for 14 days. The method, however, is inconvenient and unsuitable for tropical fruits or tomatoes. Vapour heat treatment, another method considered, injures many fruits and has therefore received only slight attention [3, 10].

Reports from America indicated that a two-hour fumigation with ethylene dibromide was most promising, so research work was concentrated on the use of this material. It became clear after a number of tests that the Queensland fruit fly is more resistant to ethylene dibromide than are the species concerned in America: for complete sterilization higher dosages had to be used. The work is being continued, and there is every hope that ethylene dibromide treatment will be accepted by quarantine authorities at home and overseas for sterilizing fruit exposed to the possibility of infection [3].

FUTURE WORK

There are two important questions: shall we try to eradicate fruit flies or be content to contain and control them? The answers are considered to be eradication for the introduced Mediterranean fruit fly and control for the native Queensland fruit fly.

Some relevant facts, taken together, give hope

that the Mediterranean fruit fly can be eradicated from the present infested area. First, there is no record that the fly has attacked a single native Australian fruit, so its distribution appears to be limited to areas of commercial fruit production. Second, the elimination of the Mediterranean fruit fly with existing control measures was demonstrated in Florida in 1956. The effort and cost of eradication in Australia will not be small, but in the long run must be considered well worth while.

The Queensland fruit fly presents an entirely different problem. It breeds in a large number of native hosts and is thus not confined to orchards. The extent and nature of the terrain in which it exists makes eradication impracticable. It is on this particular species that most of the future research work must be concentrated. More information must be obtained on the habits and ecology of the fly to assist in the battle to limit its spread, to make quarantine measures more practicable, and to make eradication campaigns in limited outbreak areas more effective. Indirect methods of attacking fruit fly populations, either by biological control, release of sterile males or other means must be established.

Better lures and cover sprays are required to protect fruit in the orchard. Sterilization treatments for harvested fruits must be perfected to overcome restrictions within Australia and to safeguard and expand markets overseas.

ACKNOWLEDGMENT

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APHIDS AND APHICIDES

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Aphids of bewildering diversity cause severe losses in a wide range of crops, partly through mechanical damage but mainly through virus transmission. Fortunately, many aphicides presenting a choice of suitable properties are now available and can be applied to the aerial parts of the crop, to the seed before planting or directly to the soil. Their selection demands attention to ecological as well as economic factors.

Aphids are plant sucking insects belonging to the Order Hemiptera, Sub-order Homoptera. In economic entomology the term can conveniently be extended to include those groups containing the *Phylloxera* of vines and the *Adelgids* found on conifers, although this would not necessarily meet with the approval of the strict systematist. In popular parlance such terms as greenfly, blackfly and dolphin are still current and the occasional use of the term 'blight' is a tacit recognition of the occurrence of epidemics. Some of the best-known aphids, at least in the Northern Hemisphere, are the black aphid of broad bean, the woolly aphid of apple, the *Phylloxera* of vine and the miscellaneous collection of greenfly on roses.

The type of damage caused can vary according to the species of aphid and host concerned, and is influenced by a number of ecological and economic factors. Some of the most serious losses are associated with virus transmission, aphids being notorious vectors of plant viruses. All aphids, however, exercise some adverse effect on the host even in the absence of viruses. The reaction to feeding may be simply a reduction in vigour, wilting or necrosis at the point of penetration, or it may involve more profound changes, such as leaf curling and even the production of galls. Honeydew (dried liquid excreta with a high sugar content), which is produced in profusion by most species given to the production of dense colonies, is unsightly, attracts ants, wasps and other insects, and encourages saprophytic fungi; it disfigures any object on which it may drop. Nuisance in the sense of personal discomfort can be caused by migrating aphids or by aphids falling from shade trees such as birch, oak, beech or walnut. Their presence on vegetables in the shop reduces acceptability to the customer.

Potential crop losses directly attributable to aphids over the world as a whole must be well in excess of £100 million per annum and the cost of control measures in current use must run into

several million pounds. Even approximate figures for total losses are difficult to get since few individual cases have been studied in sufficient detail. Those which have been investigated indicate the magnitude of the problem in the temperate zone where aphids tend to be most injurious. Strickland [12], reporting on a detailed 10-year survey of mealy cabbage aphid on Brussels sprouts in the United Kingdom, states that on average damage to the unprotected crop could reach £1 million per annum, exclusive of losses due to virus. Hull [4], reporting on a survey of "virus yellows" in sugar beet in Great Britain during the period 1946-58, estimated the average annual loss due to this aphid-transmitted virus at 0.92 tons per acre, or about 8½% of the crop. Some idea of the economic significance of aphid-transmitted viruses in the potato crop is conveyed by the bald statement that 352,500 tons of seed potatoes were "exported" from Scotland to England and Wales in 1960.

Although aphids appear to be a homogeneous group, they do in fact exhibit a bewildering variation in important biological features. It is essential therefore that the application of control measures, including those involving the use of an aphicide, should be sufficiently broadly based to allow for the biological peculiarities of the particular aphids involved. It is the purpose of this paper therefore to discuss the selection and use of aphicides in relation to the biology, especially the ecology, of the aphids concerned.

APHID BIOLOGY

Aphids are exclusively plant feeders. Their mouthparts are adapted for piercing plant tissues and include a long, flexible tube-like structure known as the stylet. With this organ, which generally penetrates into the phloem, the insect secures its food in solution. The aphid itself makes little or no contribution by way of sucking, the liquid being released by the turgor pressure within the plant. Injection of saliva, sometimes phytotoxic,

may accompany penetration. The site of feeding may be the leaves, flowers, fruit, stem, trunk, tap root or fine roots, in fact any part of the plant.

Some degree of host specificity is a characteristic of all aphids. The majority of species are found on angiosperms but some infest conifers and ferns. In many cases there is a seasonal alternation of hosts, typically involving shrubs or trees in the winter and herbaceous plants in the summer. Many species however are confined to a single host, or a group of hosts, without any suggestion of alternation.

The method of overwintering can have an important bearing on control measures. Many aphids overwinter as eggs on shrubs or trees, the eggs hatching in the spring to give rise ultimately to winged forms. Other aphids overwinter as adults or immature forms. In some cases, both methods of overwintering may exist side by side, the balance being determined by climatic or other ecological factors.

The reproductive capacity of aphids is enormous. Parthenogenesis (virgin birth) is the common method of reproduction but some species produce sexual forms in the autumn. These sexual forms are responsible for the eggs laid on the winter hosts. Parthenogenetic reproduction has a two-fold significance. Firstly, the potential productivity of each female is doubled in the first generation by the elimination of males. Secondly, since colonization of fresh hosts is in any case a very hazardous affair, the additional hazard introduced by sexual reproduction, requiring the nearly simultaneous arrival of a male, is neatly obviated.

The broad facts of aphid migration have been known for many years but only now are we beginning to understand the more fundamental principles, largely through the work of Johnson [6] and Kennedy [7]. Winged females (alatae) normally take to flight only when the meteorological conditions are favourable; among other desiderata, the wind speed must not be too great. However, once the insects have taken off they may encounter higher winds and be swept along involuntarily. In this way, alates may be transported for many miles. Alightment on plants, which demands relatively still air, is facilitated by a phototaxic response towards light from the green-yellow-orange part of the spectrum, particularly yellow light. There is no special attraction towards specific host plants. The process by which the true host plant is recognized is unknown but depends in part on the probing of tissue which

follows alightment. The evolution of dispersal and migration behaviour in aphids is related to seasonal changes in the suitability of host plants and development of parasitism and predation.

Biotic factors play an important part in controlling aphid populations. More significantly, they are becoming increasingly recognized as vital in commercial aphid control practice. Coccinellid (ladybird) grubs and Syrphid (hoverfly) larvae, for instance, are voracious predators capable of eliminating aphid colonies in a few hours. Hymenopterous parasites are rather less effective but by no means unimportant; *Aphelinus mali* Hald. for instance is used in the "natural" control of woolly aphid of apple. Infection by entomophagous fungi can also decimate colonies; but the development of such an infection requires a high relative humidity and is thus dependent on the prevailing weather modified to some extent by the growth of the crop which produces its own microclimate.

Most, if not all, of these biotic factors are density-dependent and are therefore incapable of exerting anything like their full effect until the aphid infestation is far advanced. In practice this means that they are potentially capable of terminating an existing outbreak and perhaps of preventing the occurrence of another in the following year. In more general terms, they stop aphids swamping world crops all the time but they cannot prevent outbreaks occurring some of the time. Further, they are least effective in dealing with non-colonizing aphids (for instance, *Myzus persicae* on many crops) and for this reason may be expected to exert a correspondingly smaller influence on virus transmission.

An aphid colony has a much shorter life than that of its host plant. Indeed, if the plant plays a part in terminating the life of the colony it may be through subtle physiological changes. Typically, a colony is founded initially by a winged female, the immediate progeny of which are generally wingless. Increasing proportions of alates are produced in succeeding generations. These disperse and the remaining aphids come under increasingly heavy predation and parasitism until the colony is annihilated. In field beans, potatoes or sugar beet, the course of the infestation in the crop as a whole is somewhat similar; the difference is attributable to the occurrence of primary colonies which run their course a little ahead of the main (secondary) infestation. The final clearance of the infestation may occur with dramatic suddenness; in fact

the heavier the infestation the more abrupt its end.

The last of the important biological features requiring discussion here is the predominance of aphids as vectors of plant viruses. The economic importance of these viruses is referred to elsewhere; of particular significance here is the observation that, within the limits of present-day knowledge, aphids as a group are responsible for the transmission of more plant viruses than any other single group of invertebrates; their fitness for this role has been very ably reviewed by Kennedy [6]. Aphids multiply rapidly; from an infested crop millions of alates can arise, causing widespread dispersal. Alightment, even on a fresh host plant, does not necessarily result in permanent settlement; short periods of feeding, with or without larviposition, may occur on a number of host plants. The probing of tissue for feeding, without larviposition, may take place on non-hosts, thus accounting for several instances where aphids are vectors of viruses of crops which they do not colonize. Aphids have a slight bias towards virus-infected plants in phototactic response, for such plants are generally yellower than healthy ones; on them, in addition, aphids appear to reproduce more rapidly.

APHIDS AS ECONOMIC PROBLEMS

The foregoing remarks on aphid biology suffice to indicate the enormous variation between different aphids in such matters as host specificity, site of feeding, reaction to feeding and sources of infestation. Different combinations of these biological characteristics in different aphids give rise to distinct aphid problems in economic entomology. Some examples may serve to clarify this point.

Field beans in Great Britain are subject to attack by the black aphid, *Aphis fabae* Scop., often when the crop is in flower. The sources of infestation, mainly the spindle-tree and snowball tree, are for the most part outside the control of the grower, whose problem is the control of black aphid with due regard to the safety of bees or other pollinators. Protection for a short period may be adequate because the plants soon become resistant. The importance of aphid-transmitted viruses in this crop is not adequately known.

Potatoes on the other hand are well known to suffer from the introduction and spread of certain aphid-borne viruses. The susceptible period is a long one—three months or so; several aphid species

are involved and relatively small populations could be dangerous. On a national scale the problem is resolved by growing seed crops in areas of low aphid activity, an expensive solution not necessarily in the best interests of the industry as a whole. In future, therefore, the problem may be tackled differently; an attempt may be made to restrict virus spread in the ware-producing areas by the use of suitable aphicides.

Sugar beet presents yet another problem. "Virus yellows" is widely recognized as a serious menace to the crop. The problems faced by the industry are: how to control the sources of infection (especially beet seed crops and mangold clamps), and how to ensure the correct spraying of threatened crops. Although the period of maximum susceptibility is only a few weeks, the crop remains susceptible at a diminishing level for several more weeks. Predators can exert an important effect and any aphicide used should therefore cause minimum harm to beneficial insects.

Alfalfa in the U.S.A., particularly in California, is attacked by the spotted alfalfa aphid, *Therioaphis maculata* Buckton. The damage is caused by the injection of toxic saliva and not by virus transmission. In past years heavy applications of organo-phosphorus compounds have led to build-up in certain districts, apparently through the depletion of predators. Nowadays the problem is regarded as one of "integrated control" requiring the use of a selective aphicide, or an aphicide used selectively, so as to ensure the continued operation of natural checks [10, 11].

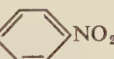
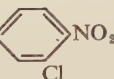
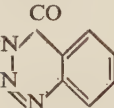
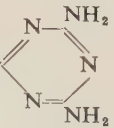
Lettuce suffer from aphid attack at various stages of growth. Infestation a few days before harvest may not affect the growth or condition of the crop but may considerably reduce its market value because of consumer distaste for infested produce. In this case the problem is the prevention or removal of infestation without leaving toxic residues. A non-toxic aphicide should be used or, if a highly toxic material is chosen, it must be capable of rapid degradation to non-toxic products.

Finally, on certain crops aphids may occur in association with other pests, for example with red spider on hops or with leaf miner on sugar beet, necessitating the use of a wide-spectrum material or a combination of a selective aphicide with another insecticide.

The above examples illustrate how the practical problem can vary from aphid to aphid or crop to crop. It may be expected that no one aphicide

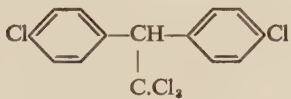
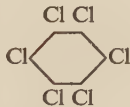
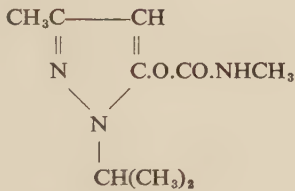
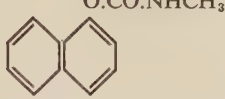
TABLE

NAMES, CHEMICAL FORMULAE AND BIOLOGICAL PROPERTIES OF SOME MODERN APHICIDES

Common Name	Structural Formula	Acute Oral Toxicity* mg./kg. (rat)	Phyto- toxicity	Systemic Properties	Residual Activity	Contact Selectivity
ORGANOPHOSPHORUS COMPOUNDS						
TEPP	$(C_2H_5O)_2PO.O.PO(OC_2H_5)_2$	c. 2	Slight	Nil	Nil	Slight
Parathion	$(C_2H_5O)_2PS.O-$ 	6-15	Slight	Slight	Short	Slight
Chlorthion	$(C_2H_5O)_2PS.O-$ 	1500	Slight	Slight	Short	Slight
Phosdrin	$(CH_3O)_2PO.OC(CH_3):CH.COOC_2H_5$	7	Slight	Slight	Short	Slight
Malathion	$(CH_3O)_2PS.SCH$ $\swarrow$ $COOC_2H_5$ $\searrow$ $CH_2COOC_2H_5$	1400-5800	Slight	Very slight	Short	Slight
Azinphos	$(CH_3O)_2PS.SCH_2-N$ 	16	Moderate	Slight	Short	Slight
Dibrom	$(CH_3O)_2PO.OCHBr.CBrCl_2$	430	Moderate	Nil	Very short	Nil
Schradan	$[(CH_3)_2N]_2PO.O.PO[N(CH_3)_2]_2$	10	Moderate	Marked	Moderate	—
Dimefox	$[(CH_3)_2N]_2PO.F$	3-5	Slight	Marked	Long	Slight
Demeton	$(C_2H_5O)_2PS.OCH_2CH_2SC_2H_5$ + $(C_2H_5O)_2PO.SCH_2CH_2SC_2H_5$	c. 9	Slight	Marked	Long	Slight
Demeton-methyl	$(CH_3O)_2PS.OCH_2CH_2SC_2H_5$ + $(CH_3O)_2PO.SCH_2CH_2SC_2H_5$	c. 100	Slight	Marked	Long	Slight
'Di-Syston' (a.i.)	$(C_2H_5O)_2PS.SCH_2CH_2SCH_2CH_3$	c. 10	Severe	Marked	Long	Slight
Phorate	$(C_2H_5O)_2PS.SCH_2SC_2H_5$	c. 4	Severe	Marked	Long	Slight
Dimethoate	$(CH_3)_2PS.SCH_2.CO.NHCH_3$	245	Moderate	Marked	Moderate	Slight
Menazon	$(CH_3O)_2PS.SCH_2-$ 	1980	Slight	Marked	Long	Good

* Mainly after Gunther and Jeppson [3], who give references to original data.

TABLE (continued)

Common Name	Structural Formula	Acute Oral Toxicity* mg./kg. (rat)	Phyto- toxicity	Systemic Properties	Residual Activity	Contact Selectivity
OTHER COMPOUNDS						
DDT		250	Slight	Nil	Very short	Nil
Lindane		125	Slight	Very slight	Very short	Nil
Isolan		54	—	Slight	—	Slight to Moderate
'Sevin' (a.i.)		500-700	Slight	Nil	Moderate	Nil
Fluoroacetamide	$\text{FCH}_2\text{CO.NH}_2$	14	Slight	Marked	Moderate	—

* Mainly after Gunther and Jeppson [3], who give references to original data.

would be ideal in all cases, much less a single formulation, or method of application. It will be necessary therefore to examine the biological properties of some of the more important aphicides.

DEVELOPMENT OF MODERN APHICIDES

Until 1939 aphid control depended largely on the use of either nicotine or quassia. The former was more effective but whether as a contact insecticide or a fumigant its application was best restricted to periods when the temperature was above 60° F. There was no residual effect. Nicotine is still occasionally used but, in recent years, far more efficient aphicides have become available.

Modern aphicides may be assigned to one or other of four groups: the organo-phosphorus, carbamate and fluorine derivatives, and the chlorinated hydrocarbons. Their names, chemical for-

mulae and more important biological properties are summarized in the table.

Historically, the significant stages in the development of aphicides were the demonstration of systemic activity of selenium by Hurd-Karrer and Poos [5] in 1936 and the discovery of the insecticidal activity of organo-phosphorus compounds by German scientists [8] around 1940. The latter discovery paved the way for the preparation, testing and marketing of a large number of chemically related insecticides with a variety of aphicidal properties. Some are rapidly lethal to insects and leave no embarrassing toxic residues on the plant; others, by their persistence, give prolonged protection to crops. They may be suitable for contact, systemic or fumigant use; for application to the foliage as spray or dust, to the soil as spray, powder or granule, or to the seed as a powder or liquid. The versatility of the group as a whole is remarkable.

BIOLOGICAL CHARACTERISTICS OF APHICIDES

Some desirable biological properties of aphicides are equally valuable in other insecticides. Thus, low mammalian toxicity to ensure safety in handling would be rated high in the specification of any insecticide; it is not a special requirement of aphicides. On the other hand, selectivity and persistence do have special significance; these properties are discussed below.

Selectivity

Selective toxicity towards aphids is a most valuable feature in an aphicide because of the high reproductive potential of aphids and the importance of parasites and predators in keeping infestations in check. An experience in the early days with parathion may be recalled. A sugar beet crop was treated with parathion, giving almost a complete kill of black aphids. Three weeks later the crop was even more severely attacked owing to heavy reinfestation and reproduction in the absence of predators. This phenomenon, now commonly referred to as a "flare up," has been recorded under a variety of circumstances, usually following the use of a broad-spectrum insecticide with little or no aphicidal activity, e.g. dieldrin and DDT. DDT, however, may be used successfully if the right conditions obtain or if repeated applications are made. Such a practice is now rightly looked upon with disfavour because of the profound effect on other insects.

Despite the high reproductive rate in aphids and the widespread use of aphicides, relatively few cases of resistance are known. It is significant that, as already indicated, investigation of such instances in the spotted alfalfa aphid in California showed that the effects were attributable to the use of non-selective materials.

Selectivity of action can also be important in preserving pollinating insects. It has been reported that field beans sprayed for aphid control have failed to give the expected increase in yield largely because of bee mortality, due to the use once more of non-selective insecticides. The inter-relationships of aphicides, bees and beans are discussed by Scriven, Cooper and Allen [9].

Selectivity can sometimes be achieved in practice with a broad spectrum material. Thus demeton as a contact insecticide has a broad spectrum but used systemically at a sufficiently low dosage it can be aphicidal with minimum harm to predators and parasites as has been shown by Stern and van den Bosch [11].

Systemic Activity

By far the most important targets for (plant) systemic insecticides to date have been aphids and spider mites. Aphids are particularly amenable to control in this way for their stylets and gut are the means by which toxic sap is injected under some degree of control. The amount of systemic chemical reaching the aphid may thus be considerable.

Effective systemic activity implies absorption into the plant by one of several possible routes and translocation to those regions, usually the foliage, where aphids feed. Few systemic aphicides are capable of moving downwards for considerable distances in significant amounts, and such a property is not so valuable commercially as movement in an upward direction. Systemic aphicides therefore, as usually envisaged at present, are characterized by upward translocation accompanied at times by some lateral movement permitting a measure of redistribution. Those compounds, e.g. demeton-methyl, which are translocated most readily tend to be redistributed most readily; toxic substance is withdrawn from, for example, older leaves where it was originally deposited and moved to the actively growing parts, including the younger leaves. These materials have an advantage when used as foliage sprays for the control of aphids in showing a marked preference for the tips of plants, especially under conditions where growth is rapid. Other chemicals—menazon is an example—are less actively redistributed and are therefore most effective when the aphids show some preference for the older leaves. A good method of getting thorough distribution with both types of materials is by root absorption or, experimentally, injection low down in the stem.

Systemic activity allows greater versatility in the use of an aphicide; the chemical may be applied to the soil, to the seed, or to the aerial parts of a crop. The systemic property may confer or reinforce selectivity and enable the toxic material to reach aphids inaccessible to contact insecticides.

Certain aphicides are able to penetrate into leaves or other plant structures and exert a localized systemic action. Parathion for instance sprayed on the upper surfaces of leaves can kill aphids colonizing the lower surfaces but feeding, of course, from the region between.

Persistence

Some aphicidal operations take the form of a "clean up"—for example, the spraying of lettuce immediately before harvest. No lasting effect is

required; in fact, chemical residues are undesirable. In the majority of operations, however, some residual effect is advantageous. A treated crop may be subject to reinfestation, or perhaps virus transmission is involved, and a more or less continuous protection is required.

Persistence can be achieved by the use of a residual contact insecticide but few compounds lend themselves to this purpose. Since the advent of systemic insecticides, however, it has been possible to secure persistence for several weeks. Earlier remarks on redistribution are apposite.

Speed of Action

Speed of action can be important in more than one respect. Occasionally a quick removal of a heavy infestation may be necessary. Generally, a grower may prefer rapid action as an assurance that the application is effective. Speed of action is usually discussed, however, in connection with virus control. It is thought that a quick kill of the vectors would considerably reduce the chances of virus transmission. Theoretically, it is highly desirable that such an aphid should be killed before it starts probing but no aphicide is sufficiently rapid in action to do this. In potatoes and sugar beet, for instance, the main objective in crop spraying is not necessarily to prevent the introduction of virus but rather to restrict its distribution.

Nevertheless, speed of action must have some importance in relation to persistent viruses, particularly where an immigrant aphid makes short sojourns, with probing, on a series of plants before finally settling down. Undoubtedly this aspect requires thorough investigation.

Toxicity

The use of systemic aphicides, as distinct from non-systemic ones, or non-systemic insecticides in general, raises problems of absorption, translocation and metabolism. Toxic material that has entered the plant may be slowly lost as vapour, excreted in guttation droplets, degraded to innocuous substances, or reduced in concentration as the plant continues to grow. Examples of each are known; but a given systemic need not exhibit them all, and they need not occur with every crop.

Since changes in flavour are sometimes associated with residues on the crop, it is essential to investigate the tainting properties of aphicides, particularly if they have localized or general systemic activity. Some organo-phosphorus compounds are malodorous in their own right, others

decompose into, or are otherwise contaminated with, mercaptan-like compounds. Tainting by their use is therefore a distinct possibility. Fortunately no serious difficulties of this kind have been encountered in practice.

Any aphicide intended for systemic use must be relatively free from phytotoxic tendencies, particularly if intended for use on or near the seed. In some cases an inherently phytotoxic aphicide can be so formulated and applied that the danger is reduced to an acceptable level.

METHODS OF APPLICATION

There is considerable freedom of choice between methods of applying aphicides; final selection depends on the particular problem and the type of effect required. For instance, a quick clean-up of aphids on plant tops is best achieved by the application of a quick-acting contact insecticide. Extended protection against reinfestation is most efficiently obtained by the use of a systemic aphicide.

Traditionally, for a quick clean-up, a contact insecticide was used, e.g. nicotine as a foliage spray at high volume rates. Dusting can give better penetration into dense crops but requires a warm day—a temperature above 60° F. When continued immigration into the crop is not involved, or is insignificant, and the aphids are exposed, such methods are permissible but not necessarily the cheapest or the most convenient. Thus a lindane or DDT emulsion correctly applied at bud-burst will give satisfactory control of oat apple aphid; there is however little latitude in timing, and an application a few days late may give disappointing results. The aphids may have penetrated into the opening bud and have become inaccessible to the spray.

In general, where aphids are concealed in curled or galled leaves, or where the foliage is dense as in hops late in the season, a material with penetrant or true systemic properties is preferable. It also facilitates low-volume application. However, the real value of a systemic aphicide lies in the longer protection it can confer. For example, whereas three or four sprayings of DDT emulsion during the season can control potato aphid to the point where the spread of leaf roll is appreciably reduced [1], a systemic aphicide may be equally effective with only two applications.

Systemic aphicides, being readily absorbed by the roots, are potentially useful in seed, tuber or soil treatments. Provided the materials are sufficiently stable in the soil, they can often give protection for long periods; they may have the additional

merit of providing protection during the emergence period when exposed foliage is too sparse for successful spraying. Seed and tuber treatment may have an advantage over granule application to the soil during this critical stage although granules, somewhat slower to take effect, may provide longer protection. Recent evidence suggests that the efficiency of soil granular treatment is very much affected by the availability of soil moisture, and is more consistently successful under irrigation.

Another technique now attracting considerable interest is the application of granular systemics to plants and adjacent soil shortly after the plants emerge. Granules lodged on the plants release enough active material to exert at least a temporary effect, while those reaching the soil (perhaps the greater proportion) have a slower but possibly stronger and more prolonged effect. Drought can again be inhibitory.

A technique that requires more investigation is the implantation of a systemic aphicide into the trunks of fruit, ornamental or shade trees. This might have advantages for large trees, especially in private gardens or public places and possibly in plantations if the trees were widely spaced. Variations of the technique, such as spraying or brushing the trunk, are worth further study.

MENAZON—A MODERN APHICIDE

The systemic aphicides already mentioned are highly efficient but none is without some disadvantage. Many have a high mammalian toxicity which may preclude their use by peasant farmers or the amateur gardener. Others are highly toxic to beneficial insects, including honey bees, and

should not be used where predators and parasites are important in limiting aphid populations or where cross-pollination is essential for maximum yields. Phytotoxicity can limit the dosage rates and methods of application of some chemicals.

At Jealott's Hill Research Station the search for improved compounds without these or other disadvantages has continued; during 1957 a new group of triazinyl phosphates was found to possess many desirable properties [2]. Related compounds in this group were synthesized and examined in the laboratory and finally in 1959 one chemical, now given the common name of menazon, was selected for full-scale field evaluation and development.

On present evidence the main advantages of menazon compared with other systemic aphicides are lower mammalian toxicity, selective action against aphids, greater residual activity and minimal phytotoxicity. It should be especially useful where beneficial insects are important in limiting aphid populations and could make the integration of chemical and biological control a much easier problem. Low mammalian toxicity—menazon is less toxic than any other synthetic insecticide in current use—makes menazon especially suitable in peasant agriculture where application methods are often primitive and operators are exposed to gross contamination by spray. Low phytotoxic hazard enables it to be used on all important crops, and it is safe for use in the soil. Menazon applied to seed or tuber is of special interest, for it shows great promise in protecting crops such as beans and potatoes against early aphid attack, preventing mechanical damage and restricting the spread of virus infection.

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CONTROL OF WORMS IN RUMINANTS BY CHEMOTHERAPY

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Many chemicals were tried for worm control in domestic animals during the nineteenth century, but a major advance was made in 1938 by the introduction of phenothiazine. The use of this material in preparations for sheep and cattle now reaches hundreds of millions of doses a year. A new chemical, methyridine, is active against many genera of worms throughout their development stages and thus approaches the ideal in anthelmintics.

Given adequate grazing space it is possible to manage a herd or flock so that the number of parasitic worm larvae on the pasture never becomes large enough to produce a heavy worm infestation. Unfortunately sufficient space is not always available. Expanding human populations and mounting prosperity lead to increased demand for meat and dairy products. More land is required for new and enlarged towns and cities. Thus the density of stocking on pastures tends to increase. New pastures are being brought into production by irrigation schemes in some parts of the world, but these are limited to countries which have suitable areas and water supplies available. Irrigation can accentuate the problem of worm control, however, by providing the moist conditions which favour the survival of larval parasites.

Even when adequate grazing space is available in normal seasons, drought may reduce the effective grazing area and bring about localized overstocking near watercourses and ponds with a parallel increase in larval concentration and hence in the incidence of helminthiasis.

When it becomes impossible to keep down the pasture concentration of parasite larvae by reducing stocking rates, anthelmintics become a necessity, and it is interesting to observe the way the gradual intensification of grazing has been associated with concomitant developments in these drugs.

EARLIER CHEMICAL CONTROL

The well-known American parasitologist Maurice Hall [14], writing specifically on anthelmintics, divided their history into three periods of some twenty to thirty years. The first of these was prior to 1881, when a large number of drugs was used quite empirically and without critical evaluation. Some were effective, but the majority were useless or even harmful.

The next period, from 1881 to 1915, was the period of critical empirical use. New and quite

useful drugs were developed, and of the older ones some were brought into favour as a result of enlightened experience. Drugs used in this period included coal-tar creosote [24], powdered areca nut and turpentine [2], which were administered in the treatment of the so-called *Strongylus contortus* infection in sheep.

The third period, from 1915 until the time Hall was writing in 1934, was that of critical experimental testing. Some new drugs were established, some older ones were standardized, but many were shown to be useless. This period might well be extended to 1938, when Harwood and others [16] first demonstrated the anthelmintic value of phenothiazine. During this time parasitic gastro-enteritis evolved as a serious disease in the British Isles, and indeed haemonchosis came to be a major threat to the sheep industry. Important factors were very probably the intensification of animal production during the first world war, and later the spread of towns into the countryside.

Copper sulphate, the anthelmintic then most commonly used, has negligible effect against immature worms and indeed little activity beyond the abomasum or true stomach, for simple copper salts are only vermicide in acid media. Nevertheless copper sulphate is very highly active against *Haemonchus* and is very cheap. It is still quite widely used in combination with nicotine sulphate for routine control of helminthiasis where the disease is not a severe problem and *Haemonchus* the most important parasite.

The first organic chemical anthelmintics were the chlorinated hydrocarbons—carbon tetrachloride and tetrachloroethylene—but these, particularly the former, sometimes produce severe toxic effects in whole groups of animals. These toxic effects appear to be closely related to diet [15], but are to some extent unpredictable.

The chlorinated hydrocarbons are only effective against worms in the bowel when swallowed

directly into the abomasum, so that prestimulation to produce closure of the oesophageal groove is necessary before dosing. In practice, therefore, each animal must be dosed twice: once with a dilute solution of copper sulphate or sodium bicarbonate according to species, and again some fifteen seconds later with the drug itself. This is obviously a clumsy and time-consuming operation, especially when large numbers of animals have to be handled, and in any case it is not very reliable.

Hexachloroethane is effective when swallowed into the rumen but only against worms in the abomasum. Like carbon tetrachloride, it is now mainly used in the treatment of liver fluke, where the route of absorption is less important than in the case of bowel worms.

PHENOTHIAZINE

The above drugs were all overshadowed, however, by phenothiazine. The ideal anthelmintic is one that combines minimum toxicity to the host animal with maximum toxicity to the largest possible number of worm genera, of which there are something like a dozen causing gastro-enteritis in ruminants. Phenothiazine came very much nearer to the ideal than any other drug known at that time.

In sheep it is virtually non-toxic: the writer has administered eight times the therapeutic dose to lambs three times in one week without producing any clinical or histopathological change. Taylor and Sanderson [25] in early trials gave some sixteen times the normal therapeutic dose to a lamb without ill effect. Reported cases of phenothiazine "poisoning" in sheep invariably prove to be the result of trauma from careless administration, which may take the form of "drenching pneumonia" due to the drugs entering the trachea, or laceration of the pharynx from the unskilled administration of tablets.

It has also been established that the administration of phenothiazine may precipitate a latent enterotoxaemia (*Clostridium welchii*) infection [17]. It is not clear whether this is specific or, as seems more likely, the result of the stress produced by gathering the sheep and dosing them.

The drug is reasonably safe in cattle—far safer than most of its predecessors—but it is not entirely without its dangers in that species.

Cattle, unlike sheep, are incapable of completely conjugating the oxidation products of phenothiazine, and one of these products—the sulphoxide—circulates in the blood stream for twenty-four

hours or so after dosing. During this period the animals become sensitive to sunlight, and to avoid severe keratitis calves must be kept in shade.

If full doses are given to weakly or emaciated cattle suffering from heavy parasitic infection, toxic systemic effects can be produced.

Phenothiazine has a wider range of activity than any of its predecessors, being highly effective against *Haemonchus* and trichostrongyles in the abomasum, and usefully so against *Ostertagia*, *Oesophagostomum* and others. It is, however, not really effective against trichostrongyles in the small intestine or *Nematodirus*, and has little if any action against the important immature stages of the worms.

In addition to its direct anthelmintic action, phenothiazine inhibits egg-laying by the female worm even when administered to the host in quantities as low as one-thirtieth of the normal dose. Thus, a small quantity may be administered in salt mixtures or food supplements put out on pastures to prevent contamination of the latter.

Considerable success has attended this method in the United States, but in other countries it has been largely unsuccessful, perhaps because animals will not readily take concentrate supplements while on good pasture. Also, it has been our experience in England that the amount of salt mixture taken by sheep may vary considerably from one year to another. In one season they may take sufficient phenothiazine in salt mixtures to control egg-laying, while in the next the amount acquired will be totally inadequate.

The so-called low dose technique of administering phenothiazine is therefore mainly restricted in Britain to the control of strongylosis in horses.

Particle Size, Purity and Safety

It was following the failure of a sample of commercial phenothiazine to control a field outbreak of trichostrongylosis in sheep that Douglas and Baker [5] showed the efficiency of the drug to be greatly reduced by the presence of an excessively high proportion of coarse particles in the powdered preparation. Gordon had shown some years earlier that coarse preparations were less efficient against *Oesophagostomum columbianum* than finer ones. In 1956 he confirmed Douglas's work [11], stating that phenothiazine particles should all be less than 30 microns in diameter and that for full efficiency the majority should be less than 20 microns.

A large number of other workers also showed

that particle size had a bearing on efficiency, although very fine micronization (below 10 microns) may reduce efficiency against parasites in the large intestine and caecum [26]. Presumably this is because a higher proportion of very finely divided phenothiazine is absorbed before it reaches the lower bowel.

Gibson [10] was unable to detect any difference in activity against pure infections of *Trichostrongylus axei* between samples of varying particle size, and the explanation was advanced that even his coarsest samples were fine enough to be efficient. That is not true. Careful examination of the figures shows that in the finest sample only 40% of the particles were less than 40 microns in diameter and, in the coarsest, only 40% were less than 120 microns in diameter. The remaining 60% ranged up to 120 microns in the finest sample and up to 280 microns in the coarsest.

It is evident that by Gordon's criteria Gibson was using very coarse material indeed, and the fact that there was little difference in activity between the samples was probably due to the small differences in particle size between them. It is particularly interesting and important that with such coarse samples he obtained an average anthelmintic efficiency of 98%.

In 1959 Douglas and his colleagues [6] in America and Forsyth [7] in Australia demonstrated the importance of purity on the activity of phenothiazine. The former found an increased efficiency of up to 15% in purified material compared with that of National Formulary specification of the same particle size. Forsyth showed that consistently good anthelmintic results required 80% purity: at less than 70% purity results were erratic or poor. A later paper by Forsyth and Scott [8] shows conclusively that purity is at least as important as particle size in determining the efficiency of phenothiazine.

The phenothiazine used by Gibson in Britain in 1951 was at least 95% pure by chromatographic analysis, whereas the material used by the workers in Australia and New Zealand about 1954 probably had a purity of not more than 75%.

The effect of the published work on particle size produced a certain amount of confusion, since, although many firms now advertise products containing fine particle phenothiazine, it is never clear from such statements exactly what the claim may mean.

There are many different methods of measuring particle size. For example, we found in one particular sample that the percentage of particles

under 10 microns diameter could be 32, 60, or 78, depending on the method used. Thus the results of field trials cannot be compared unless the method of particle size estimation is the same in each trial. It must also be remembered that commercially ground powders follow a definite pattern of particle size distribution so that all samples contain some small particles, although the number of these may be very small indeed. The usual practice of describing particle size as a percentage finer than some arbitrary figure can hide considerable variations. By contrast, the specific surface area (the surface area of one gramme of the powder) is a more precise index and has the advantage of being directly related to cuticular absorption and thence to biological activity. Even here, however, the method of determination should always be stated.

For optimum efficiency Baker and Douglas [1] suggest a specific surface area of 6000–7000 sq. cm. per gramme of pure phenothiazine or at least 25,000 sq. cm. per gramme of National Formulary standard material—this latter is equivalent to a mean particle size of 2 microns diameter.

The apparent purity also depends on the method of determination. The Kjeldahl method, although still stipulated by the British Veterinary Codex, is unreliable, since it assumes that all the nitrogen in a sample is derived from the phenothiazine. In fact, nitrogenous impurities are common in the commercial product, and an impure sample examined by this method may give a better figure than a purer one. For example, in one investigation, sample A tested 98.2% and sample B 98.0% by the Kjeldahl method, whereas by a chromatographic method [13], which eliminates nitrogenous impurities, sample A tested 89.4% against 95.4% for sample B. There is evident need for definition in these matters.

The use of newer methods of phenothiazine analysis has revealed the unexpectedly high proportion of impurities contained in some Australian samples, and Forsyth has shown that these in the past have comprised up to 25% of the sample. As mentioned earlier, phenothiazine poisoning in sheep is virtually unheard of, but a few isolated outbreaks were reported from Australia and New Zealand soon after fine grinding became widespread but before standards of purity were raised. It seems possible that the micronization of impurities—mainly complex tars—may have led to their more complete absorption by the sheep and that the impurities rather than the phenothiazine itself were responsible for the toxic effect.

Micronization certainly increases the absorption of phenothiazine by the mammalian host, according to Richardson and Todd [21], by a factor of two and a half times. Shepherd [23] has reported that photosensitization can be a danger to calves for up to three or four days after drenching, as compared with twenty-four hours with the earlier, coarsely ground material.

In spite of its disadvantages, phenothiazine continues to be used all over the world at the rate of some six thousand tons each year, which is enough for three hundred million sheep or one hundred and thirty million cattle doses. Phenothiazine is in fact so good that it was twenty years—which might be regarded as a fourth Hall period—before any compound was discovered that was in any way comparable.

OTHER CHEMICALS

Toluene was tried and found to be reasonably effective against some species of worms in ruminants, but fairly toxic; it never became popular. The piperazine compounds were also introduced during this period and are highly active against ascarids. They are widely used for treating horses, pigs and poultry. Ascaridiasis, however, has a very limited geographical distribution in cattle, and does not occur in sheep. The use of the piperazines in sheep is confined to the treatment of *Oesophagostomum* infections, in which doses as low as four grammes are highly effective [12]. The most important advance was made in 1958, when Rawes and Scarnell [19] demonstrated the high efficiency of bephenium embonate not only against mature but also against immature forms of *Nematodirus* species in lambs.

During the preceding ten years or so nematodiriasis had become increasingly important as a major problem to sheep breeders, particularly in Scotland and the northern counties of England. A feature of this parasite is that the eggs overwinter on the pasture and hatch with the coming of warm, moist weather conditions in early May. Young lambs frequently succumb to the massive invasion of the bowel wall by immature parasites following the hatching of large numbers of eggs at this time of the year. The discovery of bephenium embonate was therefore important, not only because of the high activity of the drug against the adult *Nematodirus* which protects pasture from infestation in the following year, but also because of its action in killing the lethal immature forms of the worm.

Bephenium embonate is not particularly effective

against *Haemonchus* and *Ostertagia* and the trichostrongyles, but later work by Rawes and Scarnell [20] showed that the use of the hydroxynaphthoate salt much improves the efficiency of bephenium in the abomasum against larvae as well as adult worms; but these compounds are not particularly active against trichostrongyles in the small intestine.

The organic phosphorus compounds have received a good deal of attention during the past five years or so. They have a reasonably wide range of activity with some effect against immature worms. Some of them have a systemic insecticidal effect in addition to their anthelmintic action, so that the administration of a single dose may remove both worms and external parasites at the same time. Although this property may be mainly of academic interest in the case of ticks, it may well prove very important in the control of the warble fly (*Hypoderma bovis*) and other ectoparasites with a similar life-cycle. It has also been claimed that sufficient of some of these compounds may be absorbed through the intact skin and into the blood stream to exert an anthelmintic effect on parasites in the bowel. Further work on these lines, however, appears to be necessary.

The main difficulty with the organic phosphorus compounds so far has been their somewhat narrow safety margin and unpredictable toxicity. The latter is connected with their property of inhibiting cholinesterase, and appears to vary according to climatic or geographical conditions. Riek and Keith [22], for example, noted that a dose which was safe in Queensland, Australia, was toxic in Victoria, and Forsyth [9] has suggested that some pastures may contain a cholinesterase-inhibiting factor which has an additive effect to that of these drugs.

Reports have appeared on some eight or nine of these compounds, the very multiplicity of which suggests strenuous attempts on the part of the manufacturers to overcome the problem of toxicity. This certainly seems to be the major drawback in a highly promising series.

Quite recently Kingsbury [18] has suggested that certain of the organic phosphorus compounds may have a synergistic action with phenothiazine. Further work on the effectiveness and safety of this combination is awaited.

Methyridine

A unique advance in the chemotherapy of gastro-intestinal parasitism in ruminants was made

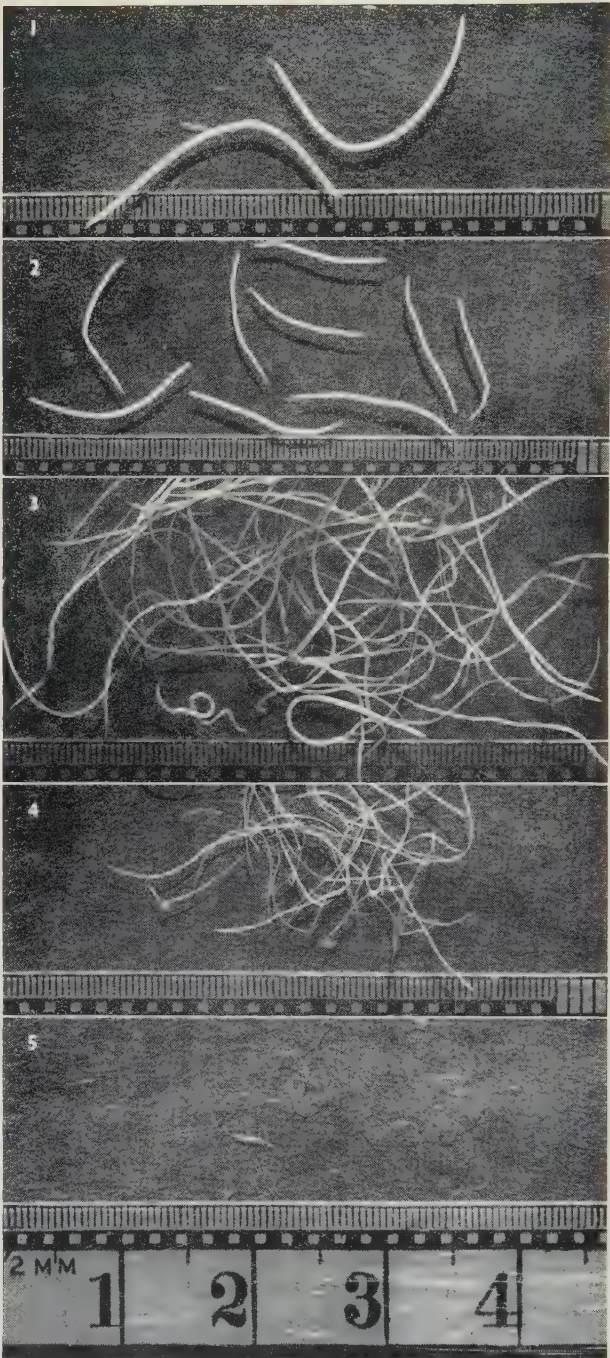
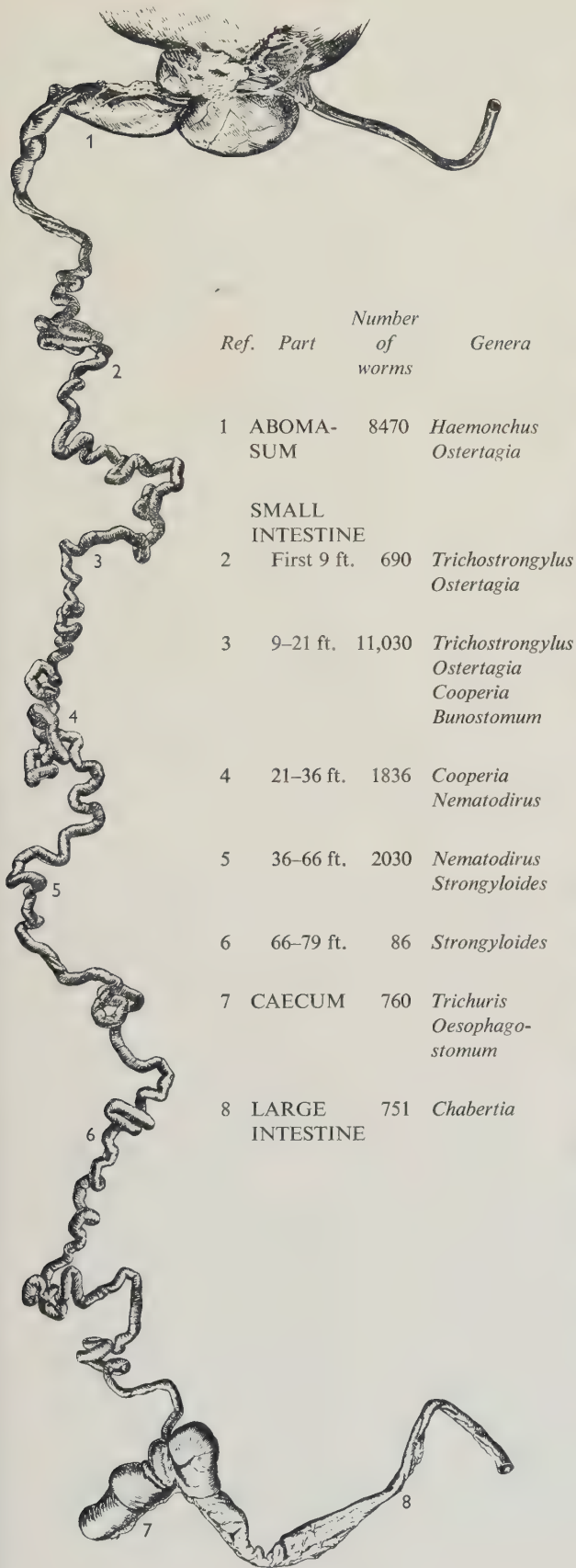


FIG. 2. Relative sizes of some worm parasites found in sheep: (1) *Bunostomum trigonocephalum*, (2) *Oesophagostomum columbianum*, (3) *Haemonchus contortus*, (4) *Ostertagia circumcincta*, (5) *Trichostrongylus colubriformis*.

FIG. 1 (left). Parasite count in various parts of a lamb's bowel.

with the introduction of 2-(β -methoxy-ethyl) pyridine, first described by Broome and Greenhalgh [3]. The coined common name of the drug is methyridine.*

An unusual feature of this drug is that after subcutaneous injection or oral administration it is rapidly absorbed and distributed throughout the tissues. Appreciable amounts pass into the alimentary canal, where they remain until metabolism in the tissues causes the blood concentration to fall, after which reabsorption takes place. Thus the drug passes from the blood stream to the intestine and back, according to the concentration gradient. Total metabolism and excretion of methyridine is very rapid, and it cannot be detected in the tissues some twenty-four hours after administration. In the event of the emergency slaughter of the animal becoming necessary after that time, the carcass may then be used for human consumption. In the case of the phosphorus compounds animals may not be slaughtered for meat for several days after the drug has been given.

The drug is excreted in the milk of lactating

cows, but in such small quantities that even at the peak level, about three hours after dosing, a man would need to drink 375 litres to acquire even an anthelmintic dose.

Because the drug passes from the blood to the alimentary canal along its entire length it comes into contact with all stages of worm species, including immature forms lying deep in the mucosa and those which lie under a protective covering of mucus. Methyridine has thus a far wider action, both as regards genera of worms and their stages of development, than that possessed by any other anthelmintic.

The pathogenicity of *Nematodirus* larvae has been noted above, but these are not the only ones that cause damage. Also the presence of adult worms in the lumen of the bowel appears in some way to inhibit the development of the fourth-stage larvae, which rapidly invade the bowel when the adults are removed. It has been said that one way to precipitate an attack of acute helminthiasis is to give a dose of phenothiazine—an over-generalization, no doubt, but true in certain circumstances. On several occasions the author has seen lambs dying from a massive invasion of immature trichostrongyles within a few days of the administration of phenothiazine. Methyridine, by removing

* The trade name of Imperial Chemical Industries Ltd. for methyridine is 'Promintic' (U.K. Patent Applications Nos. 40845/59, 40931/59 and 20099/60).



FIG. 3. Twin lambs: one reared worm-free, the other allowed to acquire a moderate burden.

immature worms at the same time as the adults, prevents this from happening.

Even in less heavily infested animals the drug has a more prolonged effect than its predecessors by reason of its effect on more than one generation of worms.

It has been shown [4] that methyridine passes through the cuticle of the worm and paralyses it by causing a neuro-muscular block. The drug is less efficient in highly acid media, probably because these favour ionization and slow down the entry of the drug, for only the unionized form of methyridine can penetrate the lipid barrier of the cuticle. It may well be for this reason that the activity of methyridine against abomasal worms is rather variable, since it is known that the acidity of the abomasum can vary widely from one animal to another. As a result, some eight out of every ten animals will be virtually cleared of worms, but the remaining two may retain an appreciable number of those that inhabit the abomasum, particularly *Haemonchus* species. The overall reduction in the worm population of the flock, however, is such that methyridine is still superior to other drugs. In ostertagiasis and *Trichostrongylus axei* infections the clinical effect is remarkably good.

Methyridine was submitted to field trial in the late summer and autumn of 1960 by over fifty practising veterinary surgeons and other workers, nearly 1000 cattle and 3000 sheep being treated. In animals acutely affected with helminthiasis—predominantly ostertagiasis and trichostrongylosis—there was a spectacular clinical improvement very soon after treatment. In most cases diarrhoea stopped in forty-eight hours or less, and appetite was restored within a few days. Rapid weight gains were shown within a few weeks. Many of the animals had failed to respond to previous treatment with other anthelmintics, such as the bphenium compounds, phenothiazine, etc.

Methyridine has no action against the liver fluke and no direct action against adult lungworms, but striking clinical recoveries have followed its administration to animals suffering with a mixed infection of bowel worms and lungworms. Some of this effect was undoubtedly due to the curing of the enteritis, but it seems possible that the drug may have some action on the pre-patent stages of the lungworm larvae.

Anthelmintics vary considerably, particularly in their toxicity, under different conditions of diet, climate and disease, and the field trials of methyridine were carefully designed in geographical

location to obtain as wide a variety as possible of types of management, breed and vegetation. Material was not available in sufficient quantity for this work until June 1960, which meant that trials in lambs on spring grass were not possible in Britain, and another series was therefore set up in Australia. Here it was possible to dose lambs from the age of six weeks onwards under conditions approximating to our own but in a variety of climates from temperate to subtropical. In order to assess the effect, if any, of lush clover pastures on the action of methyridine, trials were also set up in New Zealand. Results in both these countries exactly paralleled those obtained at home.

In a toxicity experiment 150 lambs and ewes were given double the standard dose. About one-third of the animals showed signs of incoordination, and four of the poorest animals died within four hours. By this time the remainder of the flock was again normal. Cattle given full doses showed no signs of toxicity, and when it is considered that many were suffering from very severe helminthiasis it is evident that the drug is safer than phenothiazine for these animals.

It has been noted that a local swelling may develop at the site of injection, and swellings were, in fact, reported in about one-third of the sheep and less than half the cattle involved in the trials. Swellings are rarely severe and in most cases disappear without trace; reduction of the swellings [27] is well advanced a week after injection.

Methyridine, then, probably approaches the ideal drug more nearly than any other at present known: it is particularly easy to administer, either by injection or as a drench; it has a very good margin of safety; and it has a far wider spectrum of activity than any other anthelmintic. The removal of immature worms enhances the clinical effect and reduces the necessity for further dosing, except on very heavily infested pastures.

ADMINISTRATION AND MANAGEMENT

The most effective and economical use of anthelmintics is obtained by administering them at times when it is known that an increase in worm burden is imminent. The "spring rise" in the number of eggs reaching the pasture has been noted by many authors and can be avoided by removing adult worms from the sheep a few weeks in advance. Besides removing the worm burden from the older animals, this dosing serves to protect the young from the infestation they pick up as soon as they begin to graze and which otherwise builds up

throughout the summer. Even a fairly light infestation early in life may under favourable circumstances build up into a heavy worm burden by weaning time; it is thus sound practice to dose young animals before the end of summer.

The seasonal incidence of nematodiriasis is now well established: a large number of free-living larvae become active under the warm, humid weather conditions of early May. Dosing at this time with a drug such as methyridine, which is active against immature worms, can therefore prevent outbreaks of the clinical disease. By removing adult worms as well, contamination of the pasture for the following year is avoided.

The weather during the grazing season is probably the most important single factor governing the incidence of helminthiasis. Free-living worm larvae become more active with increasing temperatures. They also require moisture for survival and as a medium for reaching the grass blades from which they are picked up by their hosts. Generally speaking, therefore, good growing weather favours larval survival. On the other hand, larvae rarely climb higher than about an inch and a half above soil level, so that lush pasture is less likely to produce helminthiasis than short grass.

The degree of infestation of an animal obviously depends on the number of larvae per pound of food consumed. If parasites are evenly scattered over a pasture, the smaller the area that an animal has to cover to obtain its daily requirements the lower will be its larval intake. The acquired worm

burden will be all the greater if the pasture is short, for then the animal must bite down closer to the ground, where the highest concentration of larvae is to be found, and also graze a wider area.

Drought conditions, while they may be responsible for the death of large numbers of parasites by desiccation, may nevertheless favour helminthiasis by causing animals to graze over limited areas in the vicinity of ponds and streams where the grass growth is better. It is evident that intelligent observation, not only of the condition of the animals, but also of weather conditions, can be a valuable aid to reducing parasite problems by the tactical use of anthelmintics.

A further possible means of controlling parasitic worms is the stimulation of an immunity by vaccination. This is already practised in the case of lungworms in cattle, but much more research is needed into the mechanism of immunity. It seems possible that the simplest means of producing immunity may be controlled, deliberate infection followed by dosing at the proper time with a highly efficient anthelmintic.

Although by good pasture management and the intelligent use of drugs, worm infestations can be greatly reduced, their presence still costs the agricultural communities of the world many millions of pounds and wastes much animal food required for human consumption. Increasing knowledge of the ecology of helminth parasites and the reaction of the animal body to them, together with the discovery of more active anthelmintics, are helping to solve the problem of worm control.

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CONTROL OF WORMS IN RUMINANTS BY PASTURE MANAGEMENT

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The use of chemicals to control helminths has aimed at eradication of the parasites and has certainly reduced population numbers. Nevertheless, control by deliberate stimulation of immunity in ruminants, following moderate exposure to infection, is still important and involves principles derived from experimental epidemiology that should not be overlooked by the farmer seeking guidance in managing pastures and stock.

There is something intriguing in the idea of bringing parasites under control through a mere change of agricultural procedure, by managing things so cunningly that the parasites destroy themselves. This seems to flatter our intelligence in a way that would not be occasioned by the use of poisonous substances that kill wherever they go.

What has the specialist to say about the prospect of controlling parasitic worms by pasture management? There are times when he should leave his laboratory and explain to fellow scientists or farmers how he came to make a useful discovery, and other times, less pleasureable, when he should give the reasons for his failure to achieve something that on the face of it seemed easy. One could imagine the practical farmer asking: "Precisely what can the veterinary helminthologist do for me? This biological knowledge may be very interesting, but is it of real, practical value? Can't it be boiled down to a few hard facts or rules of thumb, ready for use by the simple man?"

Helminthic disease among grazing animals provides an attractive subject for attempted control by changes in management, as the life histories of the parasites afford opportunities for ingenious alterations that could prevent their increase, or even eliminate them altogether. The outstanding peculiarity of all parasitic worms in this respect is the necessity for successive generations to be transferred from one host to another, individual parasites passing through developmental stages in the field, where they may be killed, or left to die, while the grazing animals move on to clean ground.

In this article it is proposed to examine the situation in the light of present knowledge, and to determine what the possibilities may be. The discussion will be confined to the three main diseases: parasitic gastro-enteritis and fascioliasis in sheep, and parasitic bronchitis in cattle.

The first of these is complicated through association with a dozen or so species of parasitic worms,

present in varying proportions at different times, each with peculiarities of life-history and environmental association. There are, however, marked similarities between the various members so that the group may reasonably be considered as a whole.

IS ERADICATION PRACTICAL?

Previous Successes

The idea of eradication is in the air at the present time through our success with bovine tuberculosis, although this disease was eliminated while some of the causal organisms still remain in Great Britain. Another instance of the same kind is the elimination of gapes from poultry. Once the most troublesome disease of chicken rearing, gapes disappeared when for an entirely different end a change was made in managerial procedure. Even more satisfying is the complete eradication of *Psoroptes ovis*, the cause of sheep scab, the last remaining parasite having been killed in Herefordshire by the use of benzene hexachloride in February 1952 [15]. It can be seen, therefore, that eradication is sometimes practical. There is, in fact, one example of the eradication of a parasitic worm from grazing animals—that of the nodular worm *Oesophagostomum columbianum* from the Province of Quebec. This is mentioned by Swales [9] as beginning, and in a private communication from T. W. M. Cameron as having been completed. Sheep are housed throughout the winter in that region and the pastures are sterilized by the cold, which the larvae of *O. columbianum* cannot withstand. When treatment with phenothiazine was found to be 100% efficient in clearing these parasites out of the sheep, a regime was introduced on an area basis for the period of winter housing; as a result, after repetition for a few seasons, this very troublesome parasitic worm was eradicated, although the use of phenothiazine at other times of the year had little effect. *Haemonchus contortus*

is similarly placed, treatment with phenothiazine being highly efficient, and the free-living larvae being unable to withstand severe cold.

These achievements are encouraging and the advantage taken of the sterilization of pastures by very low winter temperatures may well be regarded as a procedure of pasture management. In England, however, where winters are much less severe, we must look for other aids and consider how to exploit the following facts: that new-born animals are free from infection; that they can be reared in buildings away from their parents; and that the infection of pastures is of limited duration. In our approach we should first consider, not the eradication of these parasites from the whole country, but the possibility of eradicating them from a farm.

Duration of Pasture Infection

According to numerous observers, the species of parasitic worms responsible for gastro-enteritis vary considerably in reaction to climatic conditions. Some, like *H. contortus*, find it difficult to get through the winter; others, like *Ostertagia ostertagi* [6], are able to survive for periods of two years or even longer.

In parasitic bronchitis the situation is a little easier, most observers having found the free life of the larvae of *Dictyocaulus* to be comparatively short. As, however, experimental observations in the West of Scotland [3] have shown that a few larvae may be able to survive the winter, it is not possible to rely on the sterile condition of pastures that have been rested for no more than six months.

Fascioliasis is peculiar in that the development of the parasite may be suspended at three entirely different points during the life-history: as an egg; at any period during development within the snail intermediate host, *Lymnaea truncatula*; and as an encysted cercaria on the grass. These periods together cover more than two years, and when we take account of the part played by the rabbit in keeping the snails infected, we see that it is hopeless to wait for an infection of fluke to die out when the snail is present.

Infection within the Animal

Parasitic worms live sheltered lives in which everything is done for them. Food is brought to them in plenty, or they are bathed in it; they enjoy a perpetual summer that is never too hot; they are protected from predators or from any untoward influence that might disquiet them. It may not seem surprising, therefore, that the life span of

some of them may equal that of their host. There are several records of tapeworms, hookworms and flukes in man living for 10, 20, 30, or even 40 years [10], and the ordinary liver fluke of our farm animals seems to be able to continue producing its 4000 or 5000 eggs daily throughout the lifetime of the host [5]. Such long life, however, is dependent on non-intervention. In parasitic bronchitis and parasitic gastro-enteritis a change eventually takes place in the attitude of the host, which ceases to tolerate the parasites, becomes resistant, and expels most of them. Nevertheless, a few worms are always left behind in animals suffering from parasitic gastro-enteritis and may live for months or years, while in parasitic bronchitis the phenomenon of inhibited development occurs [12]: minute worms may be carried by animals for months before growing to maturity and infecting pastures.

In addition to this depressing information there are the difficulties of ascertaining when a field is free from infection and safe for worm-free stock, and when an animal can be relied upon not to disseminate infection. Eradication of these parasites seems virtually impossible; at the present time the attempt would be a waste of effort, and worse than that, it would introduce new dangers, as will be shown later. Success may eventually depend on the introduction of a system of zero grazing incorporating the principles of hygiene, animals being fed on herbage that is free from faecal contamination.

If, then, we cannot get rid of the parasites, we must consider how best to live with them.

THE ECOLOGY OF PARASITIC WORMS AND STOCK

Living with Unwanted Guests

Those of a philosophical turn of mind would doubtless agree that the best approach to the unfortunate necessity of having to live with congenial people is to get to understand them; that is our position in the matter of tolerating parasitic worms on the farm. One of the fundamental considerations for the successful development of a parasitic form of existence, at least as far as helminths are concerned, must have been that of avoiding injury to the host. If the host were to die then the whole parasite community would die along with it. This essential limitation of the populations of parasitic worms is brought about in an automatic way, a better understanding of which might enable us to assist natural forces and thus make adjustments to control worm numbers.

The extent to which the pasturing area is seeded with the eggs and larvae of parasitic worms is truly amazing. A sheep that is carrying quite an ordinary infestation of gastro-intestinal worms distributes daily some 500,000 eggs [14], so ensuring that there will be potential guests wherever there are potential hosts; but the process was geared to primitive times when hosts were sparsely scattered over wide areas, not to modern conditions in which stock are crowded on enclosed pastures. When we consider that parasitic worms of this kind tend to increase as the square of the number of animals on a standard area [11], we can speculate that a powerful factor must save the hosts from having too great a burden to bear. This factor is the immunity reaction, and equilibrium is brought about by the tension between excess of infection on the pastures and ever-increasing resistance of the hosts.

Grazing Behaviour checks Parasite Increase

The diet of animals whose grazing is restricted to small fields might well be regarded as a disgusting mixture of food and faeces, such as would cause the hygienists to hold up their hands in horror—it is also disgusting to the animals themselves. Horses, for instance, have a marked hygienic sense and a developed behaviour pattern that is highly effective in enabling them to avoid contaminated food [13]. If left in a field to themselves they divide the area into two distinct parts, one for feeding and one for defecation. Ultimately the amount of infective material on the defecation area is hundreds of times greater than that on the feeding area. Cattle show the same disgust at the presence of faeces in the grass, but their hygienic responses are less highly organized, in that they make no attempt to localize contamination, although the tufty nature of cow pasture clearly indicates the careful way in which they avoid food that is already contaminated. Sheep, on the other hand, appear to be devoid of any instinctive reaction of this kind and readily eat the grass in the immediate proximity of their own faeces.

These differences in be-

haviour possibly refer to the wild environment of long ago, when horses and cattle grazed in herds in the lowlands, and sheep were scattered over large areas of poor mountain pasture in which their opportunities for picking up infection were relatively slight. The ecological bearing of the reaction of disgust on host-parasite balance is worthy of more attention. It seems safe to assume that horses grazing in company with other kinds of stock are exposed to a greater risk from helminthic infestation than are those which have paddocks to themselves, because the areas of rough, untouched herbage are then not allowed to form and the horses cannot recognize where to defecate and where to graze. Perhaps other useful points of a like kind might be found if more attention were given to studying the behaviour of animals on pasture.

Grazing by Adult Stock checks Parasites

Adult stock may be used as vacuum cleaners on pastures. Horses, now unfortunately rare animals on the farm, clean up the pastures for sheep and cattle, eating off the larvae and destroying them [14]. Cattle do this for sheep, as far as lungworms are concerned, and sheep for cattle, hence the benefit of mixed grazing for these animals. That adult stock do the same for the young is less easily understood. It may not be so efficiently done because some larvae are put back in exchange for those picked up, but the number eaten is greater than the number disseminated and the overall effect is to clean the ground. The figures in the

TABLE
BENEFICIAL EFFECT OF GRAZING RESISTANT ADULT SHEEP ALONG WITH
SUSCEPTIBLE LAMBS, IN REDUCING THE LARVAL CONTENT
OF THE HERBAGE

	Lamb	Ewe	Total
Daily output of eggs	2,049,000	436,000	2,485,000
Resulting larvae, where 1 egg in 1000 reaches the infective stage	2,049	436	2,485
Daily intake of larvae	1,050	2,100	3,150
Resulting daily increase or decrease of larvae in herbage.	+999	—1,664	—665

The basis for these calculations is as follows: lambs pass 3 lb. faeces containing 1,500 eggs/g. and ewes 4.8 lb. containing 200 eggs/g.; lambs eat 7 lb. and ewes 14 lb. of grass per day; the grass contains 150 larvae/lb.

table summarize the results of many observations made under farming conditions. They show that the grazing of adult animals modifies the concentration of infection on the pastures and that, contrary to what has generally been held, it is advantageous to have mature and young animals together.

Acquired Resistance of Hosts the Mainstay of a Balanced Community

The tension that exists between a potential for enormous increase, such as would kill all the hosts, and a force for complete elimination that would annihilate the parasites was so adjusted in the primitive state of sparse grazing on a wide range that young animals received a small number of worms, sufficient indeed to achieve the biological objective of reproducing the species, but kept within bounds by resistance factors.

The mechanism of resistance is extremely complex and has been the subject of investigation by bacteriologists, virologists, and protozoologists since the time of Pasteur. Only recently, however, has it begun to attract the urgent attention of helminthologists, though the importance of an immune response in maintaining the health of host animals has long been abundantly clear. The reason may be found in the indefinite results that were obtained when bacteriological techniques were applied to highly organized forms of life, such as the helminths. It seems that the protective reactions are stimulated only by easily destructible products of the living parasites, a point which no doubt escaped observation because of the great difficulty in maintaining parasitic helminths in laboratory culture. One thing seems tolerably certain, however: the immune mechanism of the host is brought into operation almost entirely as a result of infection with the parasites and depends only to a very slight degree on the state of nutrition or the age of the host.

This mechanism acts on the parasitic worms in several ways. All of them may be eliminated; a large proportion may be eliminated, but a considerable number may be allowed to remain while the acquisition of further infection is prevented; egg-production of existing worms may be restricted; the development of larvae already in the host may be inhibited although these are allowed to remain and to carry out some of their normal migrations; or larvae present in tissues may be surrounded by a fibrous cyst wall from which they cannot escape.

Host-parasite Balance in Operation

The preceding paragraph may be adequate to indicate the complexity of the mechanisms that have evolved to ensure the continuity of parasite and host living on pasture together.

The operation of the system is seen to advantage in parasitic bronchitis of bovines, a severe and often fatal disease caused by the lungworm *Dictyocaulus viviparus*. In a field of beef cattle where the calves are running with their dams this parasite is almost certainly there as well, having been carried from one pasture to the next by infected yearling or two-year-old animals. Very soon after the calves have begun to sample the grass they pick up their first infection, perhaps a dozen or a score of larvae, which, proceeding with their normal development, migrate through bowel wall, lymphatic glands and blood stream to the lungs, and in so doing set in action the defence mechanism. Defence development takes time, so that the first generation of worms, at least, is able to reproduce and a second generation of a hundred thousand offspring is scattered about the pasture. Before many weeks have passed, however, worms of the first generation begin to sicken; the males presumably lose their vigour, while the females are unable to maintain the fulness of their egg production and are eventually killed by specific immune substances produced by the host.

The outcome of this action and reaction is a reservoir of worm larvae on the pasture and a calf that is fitted for life in infected fields—it has, in fact, been “vaccinated.” Vaccination of this kind is not only an essential part of the process of growing to maturity, it applies also to adults which require occasional re-vaccination. If grazing animals are to keep their resistance strong enough to enable them to come safely through all the stresses of the heavy rates of infection they may encounter in moving from one enclosed field to another, they must maintain contact with the parasite to renew this power.

The same system of population regulation holds for parasitic gastro-enteritis although there are differences in detail. Carrier animals are much more usual for this disease, most adult sheep throughout their lives carrying some parasites and scattering daily hundreds of thousands or millions of eggs over the pastures. The process by which the lambs acquire the resistance that enables them to live with these pathogenic parasites is not understood. These worms in the digestive tract do not make such intimate contact with the tissues of the

body as do the migrating husk worm larvae. Again it is the young animals that are in the greatest danger, and lambs endanger lambs because they, rather than adults, are passing out the greater number of eggs.

Fascioliasis is in a different category from the previous two kinds of infection, as sheep at least appear to retain their susceptibility throughout life.

EPIDEMIOLOGY OF HELMINTHIC DISEASE AMONG STOCK

Principles derived from Experimental Epidemiology

Epidemiology may be regarded as "pathological ecology," a derangement of the normal healthy relationship of parasites and hosts. The increased concentration of grazing animals on enclosed pastures is the basic cause, leading as it does to a concentrated seeding of eggs and an increased rate of intake by the stock. What is most serious from the epidemiological point of view is that young animals may acquire a disease-producing infestation before they have time to develop immunity.

Prolonged and detailed investigations of the experimental epidemiologists [2], using the bacterial and viral infections of large communities of mice, have enabled them to reach three main conclusions. First, that the infection will never become extinct, except as an accident in a small group of mice; second, that the death rate depends in the main upon the rate of immigration of susceptibles into the community of mice; and third, that host resistance is the most important factor in determining whether an epidemic will develop. These principles are strongly supported by evidence concerning epidemics in the field, showing that wherever man or animal is forced to live within the endemic area of disease it is essential to be immunized in order to remain healthy.

Webster [15] in America carried out a similar series of observations and arrived at the same conclusions, but stated them in a different way. He grouped the types of epidemics into three categories: (a) those occurring when a virulent strain of bacteria gains access to a previously unexposed population; (b) those occurring in infected communities when dosage is increased by some environmental factor; and (c) those occurring in infected communities when population resistance is lowered.

Principles applied to Worm Diseases of Grazing Animals

These principles help us to recognize the significant points among the mass of details in our knowledge of the biology of worms in sheep and cattle, and serve as a guide in the prevention of disease.

First to be noticed is the confirmation of the virtual impossibility of eliminating worm infections from groups of grazing animals. The microbial infections employed in the mouse experiments produced an immunity reaction that is even more definite than the reactions associated with worm diseases. For this reason, and in view of the much longer life of worm parasites away from their host, it must be agreed that worm infections are very unlikely to die out.

The second epidemiological principle for special attention is the strong emphasis the experimental observations give to host resistance as the main check on epidemic disease. It seems, therefore, that our aim in the prevention of worm disease among grazing animals should be, not so much to prevent infection as to help animals to acquire it (in small doses) early in life, and so develop a resistance—in fact, to "vaccinate" them in the field. Vaccination is a precaution that should not be confined to the young; it is also important to keep the adults in contact with the infection in order that they may maintain their resistance at an adequate level through repeated re-vaccination.

If we apply Webster's classification of epidemic types to some occurrences on farms we may recognize type (a) where calves are carefully protected from infection in the farm buildings and then, as fully susceptible animals, placed on infected pasture; or where milking cows that have been using clean leys for months, and sometimes for years, are transferred to fields that have been used by infected younger animals; or again, in some types of strip grazing or folding in which the animals first move over clean ground, thus avoiding beneficial vaccination, only to come across a heavy infection that they cannot withstand at the second time over.

Type (b) is the one most commonly seen in helminthic disease among grazing animals. For example, when susceptible calves are overcrowded they infect the pasture to such a high degree that the infection rate increases more quickly than resistance can develop. Type (c) is less prevalent, but is sometimes seen in store animals during the autumn and winter, when a sub-maintenance diet

appears to re-awaken the development of dormant, immature worms already present in the host. On a better diet these would have been eliminated, as representing nothing more than a tail-end of the summer infection.

PRACTICAL CONSIDERATIONS

In the foregoing discussion it has been necessary to descend from lofty considerations of controlling parasites by pasture management, to more modest questions of living with them on the farm. We try to understand their mode of life and turn our understanding to advantage by regulating the parasites through their own methods of population control, assisting natural forces that limit parasite numbers and avoiding anything that might pull in the opposite direction.

The outstanding importance of immunization for healthy survival within an endemic area, such as that in which our grazing animals must live, has been emphasized. It would seem, in fact, if we are to accept guidance from the principles of epidemiology, that our past endeavours to eliminate infection from animals and from pastures have been entirely wrong in aim. If the importance of immunization is acknowledged, rational action would be to introduce a light infection to animals early in life by spreading worm eggs and larvae thinly over the whole farm.

This is a new view on an old problem, and the rational teaching may be found difficult to accept for, in the words of Montaigne, we consider it with "mindes endued and doubl dide with coustome." It may be true that in endeavouring to protect the young animals and the pastures from any contamination whatever (as in the old system) we have

secured an advantage by reducing the general level and extent of contamination, but surely it is better to recognize the true position and so avoid some of the dangers that originate from faulty premises.

We may see an additional reason for the lowland sheep farmer's age-old practice of frequent movement of sheep. "Never let the sheep hear the church bells twice from the same pasture," and we might continue with the injunction, "Move them on, so as to spread the infestation thinly over the farm and maintain a low rate of pick-up." The reinfection of some fields may be just as beneficial as is the reduction of infestation in others. As a result of moderate infestation everywhere, the ewes maintain resistance and the lambs acquire it before running the risk of meeting a heavy infestation too soon.

We may also see the doubtful wisdom of reserving the best and cleanest fields for the milking cows, and we may see the indication of other dangers already mentioned under the classification of epidemic types.

Helminth parasites are so well established, ecologically, in the animals and on the pastures, that there is no way of farming stock without farming worms as well. The wise farmer knows this; but he needs some principles for guidance so as to avoid straining the relationship too far. He should thus use anthelmintic treatment as an aid to pasture management, merely to limit worm populations, and look forward to the time when he can derive an added advantage from the development of new worm vaccines [4]—not as a cure-all, but as a means of preparing young animals for the strenuous and more permanent "vaccination" that is afforded by normal larvae on the pastures.

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BOOK REVIEWS

The Economic Background to Agricultural Policy. Edith H. Whetham. First edition. Pp. 147, with 26 tables and 6 figures. Cambridge University Press. 1960. 22s. 6d. net.

The authoress states that this book is intended mainly for students of agriculture. In fact, it may well appeal to a much wider audience. One could wish indeed that it were required reading for all politicians who hope to deal with farming. There are many who seem to believe that the "laws" of economics can be abolished by Act of Parliament. Unfortunately, the consequences of ignoring economic principles are often unexpected. To take a simple example, wartime legislation, intended to give security to tenant farmers, resulted in abnormally low rents and, until the rules were changed, to the virtual disappearance of farms to rent. Thus legislation intended to help tenant farmers had the effect of compelling new entrants to become owner-occupiers and to find the capital to buy their farms.

This book is a useful addition to reading lists on agricultural economics. The style is perhaps a little more thoughtful and condensed than is customary in many of the textbooks used by the agricultural student. This is no disadvantage. Although subjects such as crop or animal husbandry have general principles, the teaching of them is sometimes made to sound as dull to the student as memorizing a cookery book. A subject where the student is not supplied with ready-made answers but must think them out for himself from general principles is thus an excellent discipline.

There are two ways in which a textbook of this kind can be written. The usual method is to give an historical account of policy and use it as a peg on which to hang such economic principles as seem to be necessary. In the present volume the principles form the framework, and each is illustrated by examples drawn mainly but not entirely from the United Kingdom. The latter is the more logical, but the student should first have a short course on recent agricultural history.

The book starts with an excellent chapter on the objectives of agricultural policy. This is very necessary because considerations of sentiment, strategy and economics are often confused in discussions on this topic. The remaining chapters deal in turn with demand, supply, marketing, land, labour and capital. Concepts such as elasticity, price-elasticity of demand and supply, propensity to

save and imperfect competition that often frighten the student are explained with admirable lucidity. The brief description of the role of agriculture in the "take-off" stages of a primitive but developing country is particularly well handled. The section on management is perhaps rather less satisfactory. The advice is correct, but is couched in such general terms that the student might have difficulty in relating it to practice. Hardly any mention is made of factors such as mechanization or the productivity of labour which are bound to affect profoundly the standard of living of the agricultural community. The Common Market is also omitted, but this is perhaps an unfair comment on a subject that has come into prominence so very recently.

The title of this book is *The Economic Background to Agricultural Policy*, and that is an exact description of its contents. If it had been possible to widen its scope, however, there is one further topic that would have been welcome to the general reader. The writer shows how policy operates but seldom ventures a comment on how it could or should have been directed. The policy-maker has a difficult task and often has to take decisions on imperfect and even misleading information. He must also give due weight to political considerations. In these circumstances the economist, if he is to play his part, must sometimes be willing to tell the administrator what he should do next and not merely how he should do it. It is to be hoped that Miss Whetham will feel encouraged to write a sequel on these lines.

F. G. STURROCK

Soil Conditions and Plant Growth. E. Walter Russell. Ninth Edition. Pp. xvi+688, with line and half-tone illustrations. Longmans, Green & Co. Ltd., London. 1961. 63s. net.

Soil Conditions and Plant Growth has been the standard English text on our knowledge of the soil as a medium for plant life since E. J. (Sir John) Russell produced the first edition in 1912; Sir John wrote the seven editions printed up to 1937. His son, Dr. E. W. Russell (now Director of the East African Agriculture and Forestry Research Organization), was responsible for the eighth edition and rewrote and recast most of the text to deal with advances in the subject, maintaining the classic's high standard. In the preface to the ninth edition Dr. Russell says that he has thoroughly revised as many sections as he had time and opportunity to do, and

the rest is little altered. In effect about half of the book has been revised to give up-to-date accounts of the subjects treated. While there is no tendency to popularize scientific information, the style of writing is so clear, simple and concise that every reader can use the material presented, to the limit of his scientific knowledge.

The book illustrates the progress that is being made in soil science. Thus, from the mass of work on the properties of soil phosphorus done during the last 20 years, clear basic ideas are emerging; appropriately the 12-page section in the eighth edition on 'Soil Phosphorus' has been completely revised and now occupies a separate chapter of 35 pages. In contrast the chapter on potassium, calcium, manganese, sulphur and nitrogen compounds in soil occupies only 10 pages; it has had little revision, and its brevity reflects the little sure knowledge we have on the properties of some of the important plant nutrients that are held by soil.

For those unfamiliar with *Soil Conditions* its scope should be indicated briefly. After an historical introduction (which alone has hardly been altered since the first edition) there follows a discussion on the nutrients needed by plants and their supply by the soil. Subsequent groups of chapters deal with soil composition and properties, the microbial and animal population of soil, soil organic matter and the nitrogen cycle, and physical aspects (temperature, air, water, structure, tilth, and root development). These sections lead on to nutrient uptake and sources of plant nutrients in the soil. Perhaps the best feature of the revised chapters is the modern physico-chemical treatment of nutrient uptake and of soil processes, presented in concise accounts not easily found elsewhere. Concluding chapters are on the effects of plants on soil, on soil formation processes, soil types, soil management and cultivation, and on the control of soil fertility in practice. The book is not restricted to temperate regions, as it deals with basic principles common to all soils; tropical soils are fully treated, and there are chapters on saline and alkaline soils.

All who are concerned with using soil in agriculture, from farmers to research workers, will benefit from reading and using *Soil Conditions*. Those who are familiar with the eighth edition will find important new material and ideas in this new edition.

G. W. COOKE

Progressive Wheat Production. F. C. Schlömer, F. Wienhues, L. M. Kopetz, T. Cole, L. Lichnowsky, A. N. Sakoff and Agricultural Departments of the member firms of the Centre d'Etude de l'Azote. Pp. 388, with line, half-tone and colour illustrations. Centre d'Etude de l'Azote, Geneva. 1960. (Unpriced).

An attempt has been made in this book to cover all aspects of wheat production; the project is very ambitious and has led to oversimplification and generalization. Nevertheless the book should make interesting reading for those who wish to gain an impression of the world wheat industry.

The book is divided into two parts. The first part consists of four chapters by different authors. The opening chapter gives a very clear picture of the supply and demand of wheat and of the world wheat trade and is, in many ways, the best part of the book; good use is made of graphs and figures. The remaining three papers in this part cover the botany and genetics of the wheat plant, rotations, methods of cultivation and fertilizer requirements. One paper is in German and another in French, but each has a full summary in English. The subject matter ranges from the most fundamental morphology of wheat to be found in any elementary text, to statements that are highly contentious. One paper has a short bibliography but there is often no attempt to justify contentious statements by giving references. In other cases full experimental evidence is presented in the book itself.

The second and larger portion of the book deals with each wheat-growing country separately. Here, as in the first part, the emphasis is on Europe, particularly Western Europe, and other countries are grouped into geographical regions. This works satisfactorily though Egypt is grouped with Africa while its Pests and Diseases section covers Egypt and other countries of the Middle East.

Each country is treated under the headings: Area and Production; Cultural Practices; Fertilizers; Pests and Diseases; and Research Institutes. The sections are necessarily so brief that any information about a given country will be well known to workers in that country. As a guide to the amount and type of production and state of development of the wheat industry all over the world the book is most valuable and provides a useful work of reference.

For this reason it is distressing to find, where data could be checked, that the book contains inaccuracies. Under Australia the statement is made that

"Victoria is the largest producer of wheat . . .," supported by figures for the crop year 1956-57. The Commonwealth Year Book of 1960 records ten-year averages ending in 1957-58 showing New South Wales as the largest producer. Similarly the statement that bunt and loose smut are the most frequently encountered diseases, with stem rust among those of lesser importance, could apply to only one of the four major wheat-producing States. Take-all, which is troublesome in all States, is not mentioned though it causes losses that probably exceed those of bunt and loose smut combined. If this is a fair sample of its standard of accuracy the book must be used with caution.

With the above reservations *Progressive Wheat Production* is useful for the general reader and of value to the expert although the latter will find the almost complete lack of references most frustrating. The copious illustrations of this well-produced volume reach a high standard; some are quite outstanding.

K. J. SYMES

Tropical and Subtropical Agriculture. J. J. Ochse, M. J. Soule, jr., M. J. Dijkman, C. Wehlburg. 2 vol. Pp. 1446, with line and half-tone illustrations (5½ in. × 8½ in. slip case). The Macmillan Company, New York. 1961. 245s. net.

It is inevitable that one compares this book with the standard English work: H. F. Macmillan's *Tropical Gardening and Planting* (5th edition 1952). The first sections of both books are very similar in their handling of climate and soil; but here the resemblance ends, the older work developing more into an encyclopedia of compressed information and the newer into a textbook which seems more designed to enable students to give the correct answers in their examinations. To cover such a vast subject in a short space would necessarily lead to a somewhat didactic style, even if the authors were not university teachers; but this does not lessen the book's value for anyone interested in tropical agriculture, though it makes reading more difficult.

An example of what the reviewer means can be seen on page 27, where we are told that sunlight is measured in two ways: in gram-calories and metre-candles (lux), but hear nothing of lumens or lamberts.

Apart from the above criticism the book is admirable. The background of climate and soil is presented first with an historical summary of the various theories and then an exposé of the most recent findings; one is glad to see the important point made that soil management in the tropics is of the utmost importance in

maintaining soil fertility (p. 217) and how patch cultivation can lead to the establishment of cogon grass and the turning of rain forest into savannah. (The grass burns so freely that forest tree seeds are killed.) Why the authors use the word cogon for *Imperata cylindrica*, better known to us as lalang, is difficult to say and is another example of the point made above. Cogon is the Philippine word for this weed.

The snare of soil analysis is admirably illustrated with a quotation from Vageler's *Introduction to Tropical Soils*, where two soils, one holding the world record for tea and the other worthless, have similar analyses, a situation only resolved if "the exchangeable bases are put on a percentage basis" an exercise which clarifies the position though not the ear of the reader (pp. 109 and 110).

Each section is followed by a considerable bibliography, mostly from American, German and Netherlands sources; indeed, one gathers from this, the numerous photographers from Indonesia, and the authors' names, that most of their tropical experience must have been in these former Dutch colonies. One is surprised to find certain lacunae in these bibliographies, for instance *Efficient Use of Fertilizers*, V. Ignatieff and H. J. Page, FAO, 1958, is not mentioned, nor, indeed, is most of the FAO tropical work.

After the six introductory chapters come those on the crops: bananas and citrus, other fruits, spices, beverages (coffee, cocoa, tea), rubber and cinchona, oil crops, fibres, sugar, cereals and tobacco. They all contain concise accounts of the botany, varieties, climatic and soil requirements, culture, harvesting, by-products, analyses, and pests and diseases; the one on bananas is particularly full and useful. One notices that among the insecticides recommended for banana borer control is hexachlorocyclohexane and hopes that students and general readers recognize this as benzene hexachloride, or BHC as it is more commonly called; in all fairness it must be said that hexachlorocyclohexane is a more correct name for this insecticide.

A useful feature under all the crop headings is the list of names in other European languages, which, though usually more comprehensive than Macmillan's list, omits the Hindi, Tamil and Malay names frequently given by the older author; this is a pity, in view of the intensification of crop production in India and Malaya. There are fewer tropical crops and fruits recorded in this book than in Macmillan's, but the

information in the new work is more complete and nearly all the crops of any commercial importance are dealt with. The book is better produced than Macmillan's, with clearer diagrams and photographs; but there are some careless mistakes in proof reading. For instance, the first acknowledgment is to the Director emeritus of the Commonwealth Bureau of Horticulture and Plantation Crops (East Malling); he is known as Mr. David Akenhead but appears here as Dr. Dean Akenhead; one wonders if rise in rank compensates for change in name. Again we find Plant Protection Ltd.'s proprietary BHC powder referred to (p. 391) as "Agricide" instead of "Agroicide," and there are other similar slips. These are unimportant, but one does expect a rather higher standard in such an expensive book. Nevertheless the work is of great value and a compendium of clearly presented information on the subject; but the reader, in this reviewer's opinion, would be well advised to consider it an adjunct to, not a substitute for, *Tropical Gardening and Planting*. G. ORDISH

The Biology of Weeds (British Ecological Society Symposium No. 1). Edited by John L. Harper. Pp. xv + 256, with line and half-tone illustrations. Blackwell Scientific Publications, Oxford. 1960. 42s. net.

This publication of the papers presented at the symposium of the British Ecological Society, held at Oxford in 1959, marks a significant step in the closer integration of academic ecology with applied botany. For too long pure botanists had little or no interest in weeds, regarding them as slightly improper material for biological investigations. Applied botanists, on the other hand, were too occupied with the practical problems of weed control to consider the wider biological implications of their work. It may well be that it was the spectacular success of the hormone weedkillers which made weeds respectable: certainly this development did spotlight our ignorance of the basic biology of weeds; it also caused highly significant changes in the distribution of agricultural weeds. Almost overnight the scarlet poppies and the yellow charlock disappeared from the landscape, and in this new situation other weeds, previously less important, slowly became more troublesome. Farming practices too have changed markedly in the past fifteen years. All this has presented an exciting challenge to plant ecologists as well as agricultural botanists, and a measure of their response is seen in the 25 papers that comprise this book.

In the opening section Dr. H. Godwin reviews the history of weeds in Britain from the Glacial Period onwards and shows how indigenous species were permitted to spread and how the flora became enlarged by accidental or deliberate importations. Professor A. H. Bunting takes up the story of secondary successions with special reference to the floras of new agricultural areas in the tropics. On a lesser scale Dr. H. Leith examines the patterns of change within a grassland community. The special taxonomic problems associated with weeds are outlined by Dr. E. F. Warburg, and three other papers deal with the taxonomy and adaptability of selected species.

Seed dormancy as a factor in the survival of weed species under cultivation is discussed by Miss J. M. Thurston. She emphasizes the importance of a full knowledge of this subject in the planning of effective cultural control; summer fallow in Britain, for instance, is largely ineffective for the control of annual species. The reservoir of dormant seed in the soil, however, has one beneficial effect: it probably slows down the development of resistance to herbicides by providing a supply of susceptible genes in the population. Dr. N. Sunderland contributes a paper on factors concerned in the stimulation of germination by substances released from plant roots. Two papers from the Official Seed Testing Station, Cambridge, deal with the dissemination of weeds by crop seeds and the need to supplement seed cleaning and other control measures by husbandry methods designed to eliminate weed plants from seed crops.

Plant competition and the interference by weeds with the growth of crop plants are covered by six studies. Dr. J. L. Harper discusses the broad ecological implications and stresses that, because of the plasticity shown by plants, numbers alone are an inadequate measure of the size of a weed population. This view is carried further by Dr. J. K. A. Bleasdale, who concludes from an analysis of the relation between weed infestation and crop yield in several horticultural crops that the use of plant weight is justified as an index of competition. Other papers are concerned with investigations into the possible role of toxic products from weeds affecting the growth of crop plants. In one of these, namely that by Dr. G. Grümmer and Dr. H. Beyer dealing with the toxic effects of species of *Camelina* on grass, there is a notable error: in Table IV the dry weight figures fail to agree with the conclusions drawn in the text.

Of the remaining subjects discussed perhaps the most interest will be found in the special weed problems created by woody species affecting grassland in Africa and New Zealand, by parasitic species on rubber, citrus and other trees in Ceylon, and by water hyacinth in the Nile.

The British Ecological Society is to be congratulated on convening a symposium dealing exclusively with the biology of weeds. It has become increasingly clear that we cannot use chemical herbicides or other control measures to best advantage unless we know more than we do at present about the dynamics of weed populations and factors affecting their invasion. The collected papers, all recorded in full, illustrate the diversity of the problems that have to be faced and provide a useful introduction to the subject. J. STUBBS

Living Earth. Peter Farb. Pp. ix + 178, with line and half-tone illustrations. Constable, London. 1960. 21s. net.

This little book has a place in the rather scanty literature of soil biology largely as an "aperitif." As an introduction to the subject for student or layman it is excellent simply because it is so readable and because the writer is able to communicate his enthusiasm for his subject through much of the book. Reading some of his descriptions of the life-cycles of insects enabled this reviewer, at least, to recapture some of the wonder which he felt in childhood, watching caterpillars pupate and butterflies emerge from chrysalids.

The first chapter emphasizes that the soil is fundamentally a biological system and a haven for many forms of life which could not exist in the hostile world outside. Chapter two gives a very brief account of soil development. In combination with the short (only three pages) last chapter, which points up the nutrient cycles, these introductory chapters give a reasonable but very superficial overall account of the soil as a biological system. The penultimate chapter deals with symbiosis (much is made of Wallin's theory that symbiosis is important in the origin of new species) and antibiosis. From the author's account the reader unfortunately gets the impression that the latter topic is exclusively the province of Waksman.

The remainder of the book is divided into three sections related to the forests, grasslands and deserts respectively. The forest section receives most emphasis (almost 40% of the book), presumably because much of it is based upon the author's own observations in New York State. He discusses the springtails, mites,

millepedes, cicadas, worms, moles and shrews. It is interesting to note that the role of earthworms in soil fertility is written down (p. 50), in this reviewer's opinion correctly so. Plant root systems, rhizosphere and mycorrhizal associations are also discussed. The role of fungi in forest soils is emphasized. His account of the slime mold is delightful. A chapter is devoted to what he calls "soil" societies, which are, however, really insect societies that happen to be in the soil.

In the grassland section he writes about bacteria and phages, nematodes and predacious fungi, wireworms and striga, emphasizing the part played by chemical diffusates in determining behaviour in the case of the latter groups. A consideration of seeds and germination leads inevitably back to insects such as harvester ants, grasshoppers, etc.

The short section on deserts deals mainly with mechanisms used by a wide range of living organisms (mesquite, cacti, the brine shrimp, kangaroo rats and honey ants) to overcome food and, more particularly, water shortages.

There are unfortunately many defects in the book. In the first place, the author's writing at times gets out of hand: it is lyricism gone mad. An example: "The trees have already shut down their water-works . . ." (p. 94). He falls into the trap of anthropomorphism on many occasions, as when he describes the destruction of their queen and larvae by the yellow-jacket wasps as an "orgy" and "democracy in its most horrible form" (p. 94). Why say "160 carloads of 50 tons capacity each" (p. 99) when "8000 tons" would do?

Secondly, the subject-matter is disorganized and unbalanced. Being an entomologist himself, the author has placed far too much emphasis on insects and other arthropods.

Finally, and most serious of all, his writing lacks scientific precision. Numerous errors and near-truths occur. For example, the activities of termites do not necessarily "enrich the soil in the vicinity of the mounds," as he states on page 85. In discussing *Rhizobium* he incorrectly states that "each bacterium is attracted only to a certain kind of plant, and no other." Finally, a horrible example of non-chemistry: "The atom of nitrogen is removed from its compound and once

again reduced to a simple nitrate in the soil . . ."

To sum up, *Living Earth* is a valiant, but not entirely successful, attempt by an entomologist to write a book about soil biology.

A. W. MOORE

The Indigenous Livestock of Eastern and Southern Africa. (Technical Communication No. 14 of the Commonwealth Bureau of Animal Breeding and Genetics, Edinburgh.) I. L. Mason and J. P. Maule. Pp. xv+151, with 179 half-tone illustrations and 3 maps. Commonwealth Agricultural Bureaux, Farnham Royal, Bucks, England. 1960. 45s. net.

In recent years several works have appeared which deal with the domestic livestock regarded as being indigenous to the African continent. While this is a very welcome development, it has obviously caused the authors to have some misgivings about publishing the present volume, as they are at pains to point out early in their introduction. The apologia is, however, quite unnecessary; this is not only the best-produced book, it is also the most comprehensive of those that have so far appeared. It is a sister volume to Mason's earlier book on the classification of West African livestock. Because of the larger area and the greater diversity of livestock covered it is necessarily a more bulky work than its predecessor. Nevertheless it comes as something of a shock to discover that practically everything that can usefully be said, at present, about the native livestock of this large and pastorally important part of the African continent is comfortably fitted into 120 pages of text. The book itself may do something to remedy this state of affairs if it prompts people on the spot to challenge the authors' temerity in writing without much first-hand knowledge of the livestock by producing some accurate data themselves. Undoubtedly the authors would feel well rewarded if this proved to be the case.

In addition to the territories normally considered as comprising East and South Africa the book covers the Congo, the Sudan, Abyssinia and Somaliland, the last three between them containing about half the total livestock described. For cattle, sheep and goats the primary classification is based on one or two simple anatomical characters: the position and size of hump for cattle; the type of

tail and rump for sheep; the length of the ears for goats. The cattle classification will not enjoy universal favour, and the authors have wisely tabulated the differences that arise when using their own and earlier systems. Sheep have obviously presented some difficult problems, but most criticism will be disarmed by the frank admission that many of the types described fit uneasily into their class. It is, however, unfortunate that the term thin-tailed is used to describe one of the major sheep classes despite the fact that many of the types included have thick fleshy tails, so markedly different from the thin-tailed West African sheep. Camels, horses and asses are classified by distribution and principal use; pigs are only very briefly mentioned, as data on them are practically non-existent.

It is pleasing to see that, with a few exceptions, the authors have adhered to their stated intention of avoiding unrewarding arguments about the origins of the different types of livestock. Even though this means that several long-cherished notions get no support, it is a very commendable feature of the book.

Wherever possible, figures are quoted for the performance of the animals described. Most of these make depressing reading, but the figures given for growth rate and milk production achieved by cattle under good conditions emphasize the serious limitations imposed by the animals' normal environment.

A striking feature of the book is the excellent collection of photographs, carefully selected to illustrate almost every type of animal described. As noted earlier, this is a well-produced volume and bears the mark of the painstaking editing that one has come to associate with the authors. The only slight inconsistency detected is in the use of the words wool, hair and kemp in the sheep section.

Essentially this is a work of reference which will readily find its way into libraries and such institutions. At the same time one feels that it could profitably be in the hands of most individuals concerned with livestock production in Africa—if for no other reason than to ensure that they look beyond the boundaries of their immediate territories and get a wider appreciation of the range and variety of the indigenous livestock of the continent.

J. L. READ

